Ecology of Hector's dolphin (*Cephalorhynchus hectori*): Quantifying diet and investigating habitat selection at Banks Peninsula

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ABSTRACT

Hector's dolphins (*Cephalorhynchus hectori*) are endangered and endemic to New Zealand. Although their distribution and abundance have been thoroughly described, little is known about Hector's dolphin ecology. Being small cetaceans living in a cold water environment, Hector's dolphins have high energy requirements, and prey abundance and movements are often assumed to be a major driver of distribution patterns. This thesis aims to increase our understanding of Hector's dolphins in a wider ecosystem context, by quantifying their dietary preferences and investigating the influence of prey availability on their habitat selection.

Using stomach contents collected from beachcast and bycaught dolphins throughout New Zealand between 1984 and 2006 (n=63), the diet of Hector's dolphin was quantified for the first time. The dolphins were found to feed throughout the water column, with 29 prey taxa identified in total. Red cod (*Pseudophycis bachus*), ahuru (*Auchenoceros punctatus*), arrow squid (*Nototodarus* sp.), sprat (*Sprattus* sp.), sole (*Peltorhamphus* sp.) and stargazer (*Crapatalus* sp.) were most commonly consumed. Red cod contributed most in terms of mass (37%), while ahuru and Hector's laternfish (*Lampanyctodes hectoris*) were consumed in large numbers. Prey length ranged from <1 cm to over 60 cm, but the majority were <10 cm long.

To help overcome inherent biases of stomach content analysis, complementary stable isotope analysis was used to examine long-term dietary preferences on the South Island east coast. Comparison of δ^{13}C and δ^{15}N signatures of dolphins (n=42) and potential prey (n=19 species) using mixing models, revealed that bony fish contributed most to the dolphins' diet. While stomach content results showed demersal prey to contribute most over spring and summer seasons, stable isotope analysis suggested that epipelagic fish have a greater long-term contribution.

The influence of prey availability and oceanography on Hector's dolphin habitat selection was assessed at Banks Peninsula, a stronghold for this species on the South Island east coast. Concurrent dolphin, demersal prey, and oceanographic surveys were carried out offshore, alongshore, and within Akaroa harbour. For all three regions, generalised additive models indicated that Hector's dolphins strongly correlated with areas of greater red cod mass. The offshore distribution of dolphins was also associated with areas of higher chlorophyll-*a* and salinity. Alongshore, dolphins were found in areas of higher prey diversity, chlorophyll-*a*, salinity, and warmer water. The performance and feasibility of two methods for sampling the demersal prey of Hector's dolphins were assessed. Fish traps sampled a greater number of species, and were more effective at sampling the important prey, red cod. Baited stereo-video sampled greater fish diversity, but was limited by the prevailing water clarity.

This study represents the first attempt to study Hector's dolphin ecology in relation to their prey, addressing fundamental knowledge gaps in what the dolphins eat, and the role of prey availability in their habitat selection. The continued survival of Hector's dolphins relies upon the success of conservation protection measures, and an increased understanding of their ecology and habitat use will help inform spatial management objectives and future conservation tools.

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"Honorable scientists: I want to compliment you on your efforts to study my kind … I'm not certain what you expect to gain from invading my privacy. You generate numbing statistics … it merely shows that you have discovered some easy facts about me; most aspects of my life cannot be written in the language of mathematics. How can you understand me? We may seem to share certain moods, but you cannot comprehend mine … Remember, you cannot divide me into independent fragments of existence. At best you might perceive an approximation … I am, like any other being, infinite in complexity, indivisible, a harmonious whole … we shall always remain of two worlds … Therefore, enjoy the mystery – and help us endure."

GEORGE SCHALLER, THE LAST PANDA

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CHAPTER 1

GENERAL INTRODUCTION: SETTING THE SCENE

1.1 HECTOR'S DOLPHIN

1.1.1 Distribution and abundance

Hector's dolphin (*Cephalorhynchus hectori*) is endemic to New Zealand, and is considered to be one of the rarest marine dolphins. Analysis of mitochondrial DNA has indicated that there are four genetically distinct populations of Hector's dolphins throughout the country: South Island west, east, and south coasts, and the separate sub-species *C. hectori maui* on the North Island west coast. Each population is regarded as isolated despite a lack of geographical barriers between them (Pichler et al. 1998, Pichler 2002). This isolation was suggested as early as 1973 (Mörzer Bruyns and Baker) and is explained by the dolphins' high site fidelity and small home ranges of approximately 50 km (Rayment et al. 2009b).

Nationwide line-transect surveys have been carried out to assess Hector's dolphin abundance (Dawson et al. 2004, Slooten et al. 2004, 2006). This is estimated to be 7270 (CV = 16.2%; Slooten et al. 2004) for the South Island Hector's dolphin, and only 111 (CV = 44%; Slooten et al. 2006) for Maui's dolphin (*C. hectori maui*) on the North Island west coast. The largest population of Hector's dolphin is found on the South Island west coast, with an estimated size of 5388 (CV = 20.6%; Slooten et al. 2004). The east coast stronghold is located at Banks Peninsula, with an estimated size of 897 (CV = 28.2%; Dawson et al. 2004), and has been the site of ongoing research since 1984 (e.g. Slooten et al. 1992, Bräger et al. 2002, Gormley et al. 2005, Rayment et al. 2010).

1.1.2 Ecology

Hector's dolphins have a patchy distribution at both large and small scales (Dawson and Slooten 1988, Dawson et al. 2004, Rayment et al. 2011). They are generally distributed in waters <90 m deep (Rayment et al. 2010), and regularly enter shallow bays and harbours (Dawson et al. 2013b). Seasonal changes in their habitat use have been described at several scales. In summer, the dolphins show a preference for nearshore areas of <20 m deep, while in winter they spread further offshore into deeper waters (Rayment et al. 2010). Hotspots in alongshore density have been described at Banks Peninsula, with consistently higher dolphin densities in certain areas and seasonal preference of others (Clement 2005). Greater use of inner Akaroa harbour has also been detected during summer, along with fine-scale patterns in diurnal movement throughout the harbour (Dawson et al. 2013b).

While boat-based, acoustic and aerial surveys have provided information on Hector's dolphin habitat use, there is limited knowledge on the drivers of their distributional patterns. Bräger et al. (2003) examined Hector's dolphin habitat selection in nearshore waters of the South Island, and found preference for shallow, turbid waters during warmer months. At Banks Peninsula, Clement (2005) found some evidence of associations with oceanographic frontal zones, indicating that dolphins aggregated around steep gradients between water masses. While there appears to be some oceanographic influence on Hector's dolphin habitat selection, these and several other studies (Martinez 2010, Rayment et al. 2010, 2011, Dawson et al. 2013b) agree that abiotic factors are most likely acting indirectly, with dolphin movements being mainly driven by the movements of their prey.

Relatively little is known about Hector's dolphin diet however, based upon only a few stomach contents from the 1980s (Slooten and Dawson 1988). A few different prey species from throughout the water column have been identified, including red cod (*Pseudophycis bachus*), flounder (*Rhombosolea* sp.), and yelloweyed mullet (*Aldrichetta forsteri*) (Slooten and Dawson 1994, Dawson and Slooten 1996). Specifically, there is a lack of quantitative information, including prey size and species relative importance. Before the influence of prey on Hector's dolphin distribution can be investigated, it will be necessary to gain a more representative understanding of what the dolphins eat.

1.1.3 Conservation

The patchy, coastal distribution and philopatry of Hector's dolphin, makes this species vulnerable to anthropogenic threats. The South Island Hector's dolphin is currently recognised by the International Union for the Conservation of Nature (IUCN) and Department of Conservation (DOC) as Endangered, while the Maui's dolphin is listed as Critically Endangered (DOC and MFish 2007, Reeves et al. 2014). The current abundance of Hector's dolphin is estimated to be 27% of that of 1970 (29316, CV=0.16), before the major expansion of commercial gillnetting (Slooten 2007). Bycatch in bottom-set gillnets is the major threat facing Hector's dolphins today, and has been the main cause of population decline (Dawson 1991a, Dawson and Slooten 2005, Slooten 2007, DOC and MFish 2007, Slooten 2013). This fishing method has been carried out throughout the known range of Hector's dolphin, and the severity of this threat has been established through interviews with fishermen (Dawson 1991a), independent observer programs (Baird and Bradford 2000), and necropsies of bycaught and beachcast animals (DOC and MFish 2007).

Potential bycatch mitigation techniques fall into two main categories: gear modifications, and spatial or temporal closures. Gear modification in the form of acoustic deterrents known as pingers, has been used relatively commonly overseas, with varying levels of success (Dawson et al. 2013a). Pingers have been used sporadically in New Zealand set net fisheries but low levels of monitoring and lack of compliance has made it difficult to assess their efficacy (Dawson et al. 2013a). It is unlikely that pingers would be successful in reducing bycatch of Hector's dolphins to a sustainable level (Dawson et al. 2013a). One of the main issues involved with acoustic deterrents is the chance of habituation over long-term exposure (Cox et al. 2001). This is particularly the case where a reward, such as prey, is gained by ignoring the deterrent. Another potential risk is habitat exclusion when pingers are used extensively in areas of preferred habitat. This is particularly likely to be a risk for coastal species such as Hector's dolphins, which have small home-ranges to begin with (Dawson et al. 2013a). Widespread testing of pingers in an active fishery would be needed to ensure mitigation effectiveness. However, the risk of any bycatch during such a trial is unacceptable when dealing with small populations of endangered species, particularly when the loss of one animal could threatened the survival of the population, as is the case with Maui's dolphin (Dawson et al. 2013a, Slooten 2013).

Spatial and temporal closures aim to implement changes to fishing effort to decrease overlap with the habitat of threatened species. In situations where closures are put into effect once bycatch limits are reached, conservative limits of acceptable bycatch and high levels of observer coverage and enforcement are needed (Hamer et al. 2011, Kindt-Larsen et al. 2012). The US Marine Mammal Protection Act calculates sustainable bycatch limits in the form of Potential Biological Removal (PBR). This level indicates the maximum number of animals, not including natural mortalities, that may be removed from a stock, while allowing the stock to maintain optimum sustainable levels (Wade, 1998). For Hector's dolphins, PBR was calculated to be less than one individual per year for most areas (Slooten and Dawson 2008). Current bycatch is estimated to be on the order of 10-35 times higher than this (Slooten and Dawson 2008), and much higher still in the case of Maui's dolphin (Slooten 2013).

Spatial management in the form of protected areas has been used for mitigation of Hector's dolphin bycatch since the establishment of the Banks Peninsula Marine Mammal Sanctuary in 1988 (Dawson and Slooten 1993). The history and effectiveness of this management were reviewed by Slooten (2013), who concluded that population recovery is unlikely under current protection measures due to the dolphin's distribution extending well beyond the offshore boundary of the current fishing closures (Rayment et al. 2010, 2011). Due to Hector's dolphins' small, coastal home ranges and discrete populations, well-designed protected areas have the potential to protect a large number of dolphins. Without any fisheries-related mortality, it is estimated that populations could almost double by 2050 (Slooten 2013).

1.2 STUDYING DIET

1.2.1 Approaches to studying diet

Knowledge of a species' diet and feeding habits are key to understanding its ecological role. Diet can be studied using a variety of methods, ranging from opportunistic to systematic sampling, across a scale of invasiveness. Traditionally, the remains of ingested food have been directly identified and measured using techniques such as stomach content and scat analysis (e.g. Ward 1970, Treacy and

Crawford 1981, Gales 1988, Tollit et al. 1997, Bulman et al. 2001, Barrett et al. 2007). In recent years, biochemical analyses have been developed to allow diet to be inferred from the signatures of stable isotopes (e.g. Hobson et al. 1994, Kelly 2000, Crawford et al. 2008, Clementz 2012) and fatty acids (e.g. Hooker et al. 2001, Bradshaw et al. 2003, Iverson et al. 2004, Budge et al. 2006) in a predator's tissues. Direct recording of feeding and foraging behaviour (e.g. Reinert et al. 1984, Bräger 1998, Lewis et al. 2004) can also be valuable, though observations are frequently difficult and qualitative in nature.

All approaches have their own advantages and biases (Jobling and Breiby 1986, Jobling 1987, Pierce and Boyle 1991, Carss and Parkinson 1996). Traditional methods using food remains provide information on what was recently ingested, revealing prey species or food items eaten a short time before sampling. For species that are only easily accessible for sampling in certain areas or seasons, for example at nesting (e.g. Moore and Wakelin 1997, Hedd and Gales 2001) or haul-out sites (e.g. Lalas 1997, Fea et al. 1999), this can introduce large spatial or temporal biases in the data. Regardless of sampling technology, an accurate representation of overall diet requires sampling from a variety of sites and times of year to take into account geographical, sex, age and individual differences in diet (Pierce and Boyle 1991). Unfortunately, when samples are collected opportunistically, as is the case with cetaceans, that is not always possible.

Stomach content analysis in particular, often involves opportunistic sampling of dead animals (e.g. Fooden 1964, Marsh et al. 1982, Gannon et al. 1998, Santos et al. 1999, Rowe et al. 2000, Pemberton et al. 2008), as only rarely are animals killed for the purposes of sampling (e.g. Vestjens and Hall 1977, Newsome et al. 1983, Sweetapple 2003, Belleggia et al. 2008, Morris and Akins 2009). Stomach contents of cetaceans, have in the past been obtained from animals taken by whaling vessels (e.g. Martin and Clarke 1986, Clarke et al. 1993), however samples typically come from dead animals that were bycaught or beachcast (e.g. Santos et al. 2004, Pusineri et al. 2007, Meynier et al. 2008). The rate of bycatch is linked to fishing effort and its overlap with cetacean distribution. Therefore, when stomach samples are primarily collected from bycaught animals, as is the case with Hector's dolphin, it is important to consider the temporal and spatial biases introduced.

Other biases of scat and stomach content analysis arise from the different digestibility of prey items (Pitcher 1980, Treacy and Crawford 1981, Pierce and Boyle 1991), resulting in the misrepresentation of some prey species. With marine mammals for example, cephalopod beaks may be retained for longer than fish remains (Pitcher 1980), leading to an overestimate of their dietary contribution. The main advantage of stomach content and scat analysis is the ability to gain quantitative dietary information. Food consumed can be accurately identified to species level, counted, measured, and ranked in terms of relative importance to the diet (Pierce and Boyle 1991).

The usefulness of direct observations in dietary studies depends upon the species in question. For small cetacean species, observations of foraging are opportunistic, rare, and usually limited to surface feeding (e.g. Bräger 1998, Clua and Grosvalet 2001). The main advantage of this method is that it is relatively non-invasive, however it is less likely to result in accurate, quantitative data. Food items may be misidentified or prey size misjudged, and there is usually no possibility of later confirmation (Carss and Godfrey 1996). Capturing animals to observe what they have eaten involves much more disturbance, though it does allow the collection of quantitative information such as prey number, size, and energy content (e.g. Montevecchi et al. 1992, Harding et al. 2009).

Both stable isotope analysis (Hobson et al. 1996, Kelly 2000) (discussed in detail in Section 1.2.3), and fatty acid analysis (Iverson et al. 2004, Budge et al. 2006) avoid some of the biases of stomach content and scat analyses by assessing the food assimilated by the consumer, rather than just ingested. Depending upon the tissue used and its turnover rate, stable isotopes can also provide dietary information over different timescales, from a few days with high turnover tissue such as liver, to years with bone (Tieszen et al. 1983). The range of tissues that can be examined allows this method to be applied in a wide variety of studies, including those in which relatively non-invasive techniques are preferred (e.g. the use of exfoliated skin: Lusseau and Wing 2006), and those examining palaeodiet through the use of geologically young fossils (Clementz 2012).

A drawback of these biochemical approaches is that they cannot identify which prey were consumed unless there is already some knowledge of potential prey species to include in models (Lesage et al. 2001, Iverson et al. 2007). Prey signatures must also be grouped into sources that are isotopically distinct. When isotopic signatures of potential prey are known, models (Phillips and Gregg 2001, Iverson et al. 2004, Parnell et al. 2010) can infer the likely relative contribution of prey sources to the predator's diet. These analyses are therefore, best used in combination with more traditional approaches such as stomach content analysis, as will be the case with the research presented here.

1.2.2 Introducing stomach content analysis

Stomach content analysis relies upon finding and identifying food remains (Ward 1970, Hyslop 1980, Pierce and Boyle 1991). For terrestrial predators, commonly used remains include bones, teeth, claws, feathers, and hair. For marine predators, fish otoliths and squid beaks are commonly used for identification, along with the bones, scales, spines, and shells of prey. Otoliths are particularly useful as their shape and size vary considerably from species to species (Smale et al. 1995, Furlani et al. 2007). For herbivores, commonly used plant remains include cuticle fragments, seeds, bark, and flowers.

Once remains have been sorted, identified, and measured, diet composition can be assessed in a variety of ways, each with their own form of bias (Hyslop 1980). Frequency of occurrence is simply calculated as the number of stomachs containing a food type, expressed as a percentage of the total number of stomachs examined. This approach gives no information on the relative amounts of food eaten, and is likely to over-represent species that take longer to digest (Hyslop 1980, Pierce and Boyle 1991). Food items can also be counted to give an estimate of the minimum number of each species consumed, and an indication of species' importance based upon the number of items consumed. This can over-estimate the importance of small prey, and again, those species that take longer to digest (Hyslop 1980, Pierce and Boyle 1991). Measurements of remains can be used to derive the weight of prey consumed for species where the relationship between the size of the prey item and its remains are known. Species can then be ranked in terms of importance by the mass of items consumed. This technique is widely applied with fish (e.g. Jobling and Breiby 1986).

Considerable errors can come from using partially digested or eroded remains (Pierce and Boyle 1991).

Combined indices are often used to facilitate comparison and present an overall measure of dietary importance for each food type. The 'Index of Relative Importance' (Pinkas et al. 1971), for example, represents the percentage frequency of occurrence multiplied by the sum of percentages of importance by number and mass. Such indices can compound the biases from the component methods, and are of dubious value (Hyslop 1980).

1.2.3 Introducing stable isotope analysis

Ratios of carbon and nitrogen isotopes are typically used in studies of ecology and food-web dynamics. The amount of each isotope in an animal's tissues is directly related to that in the tissues of its prey (DeNiro and Epstein 1978, 1981). By examining the isotopic composition of both the animal and its potential food items, and using source apportionment modelling (Phillips and Gregg 2003), it is possible to estimate the most likely composition of the animal's diet.

The isotopic signature of a tissue is expressed as a delta value, in this case of carbon and nitrogen, written as δ^{13}C and δ^{15}N. The delta value refers to the ratio of the heavy to light isotope compared to the same ratio in a standard, and is expressed in parts per thousand (‰) differences from the standard according to the following equation:

$$\delta X = \left[\left(\frac{R_{sample}}{R_{standard}}\right) - 1\right] \times 1000$$

Where X is ^{13}C or ^{15}N and R is the corresponding ratio ^{13}C/^{12}C or ^{15}N/^{14}N (Peterson and Fry 1987).

NSB-19 (cross-calibrated to Pee Dee Belemnite) and atmospheric nitrogen are used as the carbon and nitrogen standards respectively (Rundel et al. 1989). Marine organisms typically have negative δ^{13}C values as they are depleted in ^{13}C relative to PDB, and positive δ^{15}N values as they are enriched in ^{15}N relative to atmospheric nitrogen.

As food is assimilated into a consumer's tissues, the isotopic concentrations of the food change (Tieszen et al. 1983). The details of this change, known as fractionation, depend upon the species and tissues in question. The δ^{13}C signature changes little between prey and consumer (typically ~1‰; DeNiro and Epstein 1978), so carbon sources are especially useful in determining the source of carbon and tracing which type of primary producers support the food-web. The δ^{15}N signature is typically enriched ~3.4‰ with each trophic step (Peterson and Fry 1987) and so can be used to infer both the consumer's diet and trophic level. In order to examine the contribution of prey to the diet of a consumer, it is necessary to take these fractionation values into account. If the level of isotopic fractionation is known for the tissue type in question, then the isotope signature of a consumer's diet can be predicted using the following equation:

$$D_t = D_d + \Delta_{dt}$$

Where D_t is the isotope concentration of the consumer's tissue, D_d is the isotope concentration of the diet, and Δ_{dt} is the fractionation between diet and consumer tissue (Hobson and Clark 1992).

Controlled feeding experiments, in which consumers are fed an isotopically homogenous diet, are needed to determine the isotope fractionation between consumer and prey for a particular species. As it is not possible to conduct such studies for the majority of marine mammals, it is often necessary to use data collected for other species and be aware of the assumptions being made. Controlled feeding experiments with pinnipeds (e.g. Hobson et al. 1996), the only group of marine mammals on which such studies have been conducted (Newsome et al. 2010), suggest that fractionation values are relatively consistent across taxa, and fall within the ranges typically observed in terrestrial carnivores (see Table 3 in Newsome et al. 2010).

Isotopic mixing models use the isotope signatures of consumer and prey along with the appropriate fractionation values, to infer the relative contribution of potential prey to the assimilated diet. Over the last decade, several modelling procedures have been developed. Initially these were constrained by the number of isotopes or prey sources that could be included (Phillips 2001). New models have been developed that allow the natural complexity of ecosystems to be explored without such severe limitations (e.g. IsoSource: Phillips and Gregg 2003). More recently, Bayesian mixing models have been developed, e.g. MixSIR (Moore and Semmens 2008) and SIAR (Parnell et al. 2010), which can readily incorporate uncertainties around isotope signatures and fractionation values, and provide a range of possible solutions (Phillips et al. 2014).

1.3 STUDYING HABITAT SELECTION

1.3.1 Definition and importance

Studying habitat use and identifying the drivers of habitat selection are fundamental in ecology. For a robust understanding that can aid conservation management, it is useful to know not only where an animal lives, but why animals live where they do (Gavin 1991). Habitat is defined as any environment offering the conditions and resources that support occupancy by a species (Hall et al. 1997). Habitat *use* is the way an animal uses this environment, e.g. where and when it spends time foraging, breeding, or resting. Habitat *selection* is a process involving decisions (innate or learned) made by an animal about which habitat to use at different scales, resulting in habitat *preference* and disproportional use of some environments over others (Hall et al. 1997, Krausman 1999).

Habitat use is known to correlate with spatial and temporal factors at various scales. At broad scales, a species may live in only certain regions of the world (Begon et al. 2009, Gaston 2009, Rondinini et al. 2011), undertake seasonal migrations over large distances (e.g. Piersma and Lindström 2004, Rasmussen et al. 2007), or occur in certain habitat types more than others (e.g. Berg et al. 1994, Weber and Meia 1996, Gregory and Baillie 1998, Wells et al. 2008a). At smaller scales, patchiness in habitat use can occur in correlation with habitat characteristics such as elevation (Poole et al. 2000), water depth (Karczmarski et al. 2000, Cañadas et al. 2002), distance from shore (Rayment et al. 2010), and can differ depending upon the time of day (Moreno et al. 1996, Dawson et al. 2013b). Various environmental characteristics correlate with habitat selection, resulting in these patterns in habitat use. These include abiotic factors such as frontal zones (Johnston et al. 2005, Doniol-Valcroze et al. 2007) precipitation (Martin 2001), and wave exposure (Friedlander et al. 2003, Dominici-Arosemena and Wolff 2005), and biological factors such as canopy cover (Pike et al. 2011), prey abundance (Fauchald and Erikstad 2002, Heithaus and Dill 2006), and predation risk (Werner et al. 1983, Mao et al. 2005, Heithaus and Dill 2006).

Quantifying these patterns and identifying the associated drivers are useful for conservation when spatial management options are considered (Hooker and Gerber 2004, Bailey and Thompson 2009), and can aid in making predictions of how species will respond to environmental changes and anthropogenic disturbance (e.g. Marzluff 2001, Durner et al. 2009, Tittensor et al. 2009). In order to monitor habitat quality, the habitat selection of keystone species and top predators such as seabirds and cetaceans can be used as indicators of ecosystem health (Caro and O'Doherty 1999, Carignan and Villard 2002, Hooker and Gerber 2004, Niemi and McDonald 2004, Piersma and Lindström 2004). The benefits of understanding the drivers of habitat selection have been demonstrated in a number of applications, including the development of protected areas (Hooker and Gerber 2004, Cañadas et al. 2005) and predicting areas suitable for population expansion (Thatcher et al. 2006, Guisan et al. 2013).

1.3.2 Approaches to studying habitat selection

Habitat selection can be investigated in a variety of ways, involving the collection of data on species' habitat use, along with measurements of potential environmental drivers, such as abiotic factors and predator/prey abundance. Redfern et al. (2006) describe this process for cetacean habitat selection in a detailed review. Several techniques are commonly used to collect data on species' habitat use, including visual surveys (e.g. Forney 2000, Cañadas et al. 2002, Pratchett et al. 2012), acoustic detection (e.g. Širović and Hildebrand 2011, Baschuk et al. 2012, Dawson et al. 2013b, Costa et al. 2014), capture (e.g Wells et al. 2008a, Lindell et al. 2012), and tagging (e.g. Poole et al. 2000, Guinet et al. 2001, Roy et al. 2013). Ideally, data on environmental characteristics are collected at the same time and *in situ*, allowing a closer temporal and spatial match. This can be costly, however, and when *in situ* measurements are not possible, information can gained via remote sensing and other external data sources (e.g. topography/bathymetry).

Habitat selection can be assessed from these data using various methods, from descriptive mapping of the overlap between a species' distribution and environmental variables, to statistical assessments of influential drivers. A habitat model is a numerical representation of a species' habitat preferences. Regression models are commonly used to describe the relationship between species' distributions and one or more habitat variables (Redfern et al. 2006). Several regression methods are available, depending upon the assumptions about the distribution of the variables and the form of the relationship. Two of the most common methods, include generalised linear modelling (GLM; McCullagh and Nelder 1989), and generalised additive modelling (GAM; Hastie and Tibshirani 1990).

GLMs extend standard regression. They allow the response variable (y) to take on a variety of non-normal distributions, and use a 'link function' to establish a relationship between the mean of the response variable and the linear combination of predictor variables ($x_1, x_2, \ldots, x_n$), plus a constant, c.

$$y = c + \sum_{i=1}^{n} \beta_i x_i$$

The greater flexibility of GLMs over standard regression means they are often better suited for analysing ecological relationships. For example, ecological data can be better fitted by the Poisson distribution (with the log link function), when the response variable is in the form of a count (*i.e.*: number of individuals), or the Binomial distribution (with the logit link function), when the response variable represents presence-absence data.

GAMs extend this further and provide greater flexibility than GLMs, by not constraining the relationship between x and y to be linear. Where GLMs estimate regression coefficients $\beta_0, \beta_1, \ldots, \beta_n$, GAMs estimate smooth functions $f_0, f_1, \ldots, f_n$.

$$y = c + \sum_{i=1}^{n} f(x_i)$$

This flexibility often results in a better fit to the data, but GAMs can be harder to interpret. While the results of GLMs are typically present as tables of coefficients, the results of GAMs are interpreted from scatter plots of the estimated smoothed species-habitat relationships. They are also purely additive, and cannot represent interactions amongst predictors.

The choice of technique depends partly upon the nature of the data. Caution is needed to ensure an appropriate model is selected and all assumptions are met. This includes ensuring independence among observations, which can be violated by autocorrelation, and no collinearity among predictor variables.

Only those predictor variables thought to be important should be included in the modelling process. Rather than testing all possible combinations of predictors, it is often better to select candidate models *a priori* for comparison. These candidate models should be ecologically meaningful, based upon plausible hypotheses and previous studies (Burnham and Anderson 2002, Johnson and Omland 2004). Effort should also be made to avoid building so many models that spurious findings become likely (Johnson and Omland 2004). Once a set of models is defined, models are compared to determine which combination of predictor variables provides the best fit to the observed data. Three methods of model comparison are typically used: maximising fit by calculating R^2, null hypothesis testing, or model selection criteria. These approaches are reviewed by (Johnson and Omland 2004), who recommend the use of Akaike's Information Criterion to select models. This method considers both fit and complexity, ensures parsimony, and allows multiple models to be compared simultaneously. Akaike's Information Criterion (AIC; Burnham and Anderson 2002) is commonly used in ecology, and ranks competing models using maximum likelihood scores as a measure of fit, penalizing models of greater complexity. For a review of the use of AIC in ecology, see Burnham et al. (2011).

1.3.3 Habitat selection of small cetaceans

Studying the habitat use of small cetaceans presents several challenges. They often live in remote, deep environments, can undertake large migrations, and spend the majority of their time out of sight, underwater. As a result, sampling their distribution and abundance can be complicated and costly. Gathering data on environmental variables is also not simple. The high cost of marine equipment and resources can reduce the feasibility to sample data directly, and instead, data available via remote-sensing are often used for certain types of information (e.g. Sea-surface temperature (SST) & Chlorophyll-a concentration; Panigada et al. 2008). Such data typically cannot resolve temporal and spatial variability on a small scale, and so for localised studies of cetacean habitats, it is much better to directly and concurrently sample cetacean and environmental data if possible.

Many species show spatial or temporal changes in their distribution patterns in response to environmental variability. The distributions of small cetaceans have most commonly been studied in relation to their physical environment. Hector's dolphins have been found to be distributed closer to shore in summer, correlated with warmer water (Bräger et al. 2003) and frontal zones (Clement 2005). Likewise, the closely related Chilean dolphin (*Cephalorhynchus eutropia*) is predominately distributed close to shore, in shallow waters, near rivers (Heinrich 2006, Ribeiro et al. 2007). Overall, small cetacean distributions have been related to a variety of physical factors, including water depth (Karczmarski et al. 2000, Cañadas et al. 2002, Ingram and Rogan 2002, Hastie et al. 2003, Garaffo et al. 2010, Booth et al. 2013), seabed slope (Ingram and Rogan 2002, Hastie et al. 2003, Garaffo et al. 2010, Booth et al. 2013), sea surface temperature (SST) (Gaskin 1968, Gowans and Whitehead 1995, Forney 2000, Baumgartner et al. 2001, Bräger et al. 2003, Forney et al. 2012), and salinity (Forney 2000, Torres et al. 2008, Forney et al. 2012).

The majority of these studies hypothesise that prey availability likely plays a crucial role in cetacean habitat preference, but there is usually no quantitative data on prey to assess this. Townsend (1935) was one of the first to suggest a direct association between cetacean distribution and prey availability. This would require that cetaceans have knowledge of, or are able to predict prey distribution, and that the prey are accessible. The few studies that have data to assess this association have found varying results. The movements of both spinner dolphins in Hawaii (Benoit-Bird and Au 2003) and dusky dolphins in Kaikoura, New Zealand (Benoit-Bird et al. 2004) closely followed the vertical migrations of their prey. The abundance of dusky dolphins during a brief study in Admiralty Bay, New Zealand (Benoit-Bird et al. 2004) was also found to correlate with the availability of prey patches.

Other studies suggest that predator-prey overlap may be more complicated than anticipated. Heithaus and Dill (2002) learned that the distribution of foraging bottlenose dolphins in Shark Bay, Western Australia, reflects a trade-off between prey availability and predation risk. There was a close match between dolphin distribution and that of their prey, but only when sharks were absent. MacLeod et al. (2013) found no evidence of overlap between sightings of Risso's dolphins in Scottish waters, and the distribution of the octopus that appears to be their main prey. It is noted however, that this result could be due to untargeted sampling of both predator and prey, as well as differences between the scale used to model species occurrence and the scale at which the dolphins actually forage (MacLeod et al. 2013). Torres et al. (2008) also found that the resolution of their fish sampling was too large to describe fine-scale overlap between bottlenose dolphins and prey accurately. Overall, the scale-dependency of predator-prey relationships varies with prey patchiness and predictability (Fauchald et al. 2000, Redfern et al. 2006). In Shark Bay, for example, where prey biomass is predictable at multiple spatial scales across seasons, the distribution of bottlenose dolphins matches prey distribution well from scales of 10s to 100s of metres, in the absence of sharks (Heithaus and Dill 2006).

1.4 THESIS GOALS AND OUTLINE

The overall goal of this thesis was to study Hector's dolphins in a wider ecosystem context by identifying dietary and habitat preferences.

Specifically, I aimed to:

- gather detailed, quantitative information on Hector's dolphin diet, including potential prey species, sizes, and relative importance,
- overcome inherent biases in dietary analysis and gain a more representative understanding of Hector's dolphin diet by combining multiple methods,

- record seasonal patterns in the habitat use of Hector's dolphin throughout multiple regions of Banks Peninsula,
- concurrently quantify the availability of important prey and gather information on the physical oceanography of the surrounding environment,
- identify which factors are associated with the dolphins' distribution and have the potential to drive Hector's dolphin habitat selection.

These objectives will be addressed using a multidisciplinary approach and a variety of research methods.

In **Chapter 2**, I address my first goal by quantifying the diet of Hector's dolphins throughout New Zealand using stomach content analysis from bycaught and beachcast individuals. Published as: Miller, E., Lalas C., Dawson, S., Ratz, H., Slooten, E. (2013) Hector's dolphin diet. The species, sizes and relative importance of prey eaten by *Cephalorhynchus hectori*, investigated using stomach content analysis. Marine Mammal Science. 29(4): 606-628. In this study I analysed the stomach content remains and wrote this publication with advice from my co-authors, who provided the initial stomach content samples.

In **Chapter 3**, I extend this dietary study to examine the longer-term dietary preferences of Hector's dolphins on the South Island east coast using stable isotope analysis of bone collagen. Dolphin $\delta^{13}C$ and $\delta^{15}N$ signatures are compared to the signatures of prey species identified in Chapter 2 using mixing models to estimate the proportional contribution of different prey groups to the dolphins' diet.

In **Chapter 4**, I record the habitat use of Hector's dolphins throughout three regions of Banks Peninsula and assess the influence of both oceanography and prey availability on their habitat selection.

In **Chapter 5**, I compare results from two methods used to sample benthic prey in the habitat study at Banks Peninsula. Fish traps and baited stereo-video were simultaneously set to investigate whether the use of different sampling techniques could overcome biases in each method.

In **Chapter 6**, I summarise the results of this work, discuss what has been learned about Hector's dolphin ecology, and suggest directions for future research.

CHAPTER 2

THE SPECIES, SIZES AND RELATIVE IMPORTANCE OF HECTOR'S DOLPHIN PREY, INVESTIGATED USING STOMACH CONTENT ANALYSIS[1]

2.1 INTRODUCTION

Dietary studies provide important insight into interactions among species and help to define a species' ecological role. Such studies not only increase ecological understanding, but can prove valuable to conservation efforts by aiding predictions of how a species will respond to anthropogenic disturbance and climate change (Heithaus and Dill 2002, Grémillet and Boulinier 2009).

Hector's dolphin (*Cephalorhynchus hectori*) is endemic to New Zealand, and is currently divided into two genetically distinct subspecies (Baker et al. 2002). Hector's dolphin (*C. hectori hectori*) is distributed in three distinct regional populations throughout the South Island, and Maui's dolphin (*C. hectori maui*) is found along the North Island west coast (Pichler et al. 1998, Pichler 2002). For both subspecies, substantial population decline due to bycatch in gill and trawl nets (Dawson 1991a, Dawson and Slooten 2005) has been indicated by stochastic population viability analyses (e.g. Slooten and Dawson 2010) and loss of genetic variation (Pichler and Baker 2000). Other potential threats include indirect fisheries interactions, habitat degradation associated with aquaculture and dredging, and impacts of tourism. Knowledge of the prey eaten by the dolphins and their relative dietary importance may help to predict where and when there is potential for such interaction, and help in understanding population recovery.

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[1] Published as: Miller, E., Lalas C., Dawson, S., Ratz, H., Slooten, E. (2013) Hector's dolphin diet. The species, sizes and relative importance of prey eaten by *Cephalorhynchus hectori*, investigated using stomach content analysis. Marine Mammal Science. 29(4): 606-628.

Hector's dolphins have a very patchy distribution both between and within populations (Dawson and Slooten 1988, Dawson et al. 2004, Rayment et al. 2011). Seasonal distributional patterns have been well documented, with the dolphins clustered inshore in summer and more evenly distributed in winter (Rayment et al. 2010). Being small cetaceans living in a cold water environment, Hectors' dolphins have high energy requirements, so it is reasonable to hypothesise that their distribution will in part be driven by that of their prey. Dietary studies are the first step in investigating this link.

Hector's dolphin is one of four species in the genus *Cephalorhynchus*. All are small dolphins, endemic to coastal waters in the temperate Southern Hemisphere. They occur primarily in waters less than 150 m deep and are all susceptible to entanglement in net fisheries (Dawson 2009). The diet of the other *Cephalorhynchus* species has been described from a small number of bycaught individuals. Chilean dolphins (*C. eutropia*) have been found to eat primarily small schooling fish and squid (Torres et al. 1992). The main species found in stomach contents of Heaviside's dolphin (*C. heavisidii*) were demersal species, particularly juvenile hake (*Merluccius* spp.), as well as small pelagic fish (Sekiguchi et al. 1992). Hake was also found to be frequently consumed by Commerson's dolphin (*C. commersonii*), along with squid (Bastida et al. 1988, Crespo et al. 1997).

In this study I quantify Hector's dolphin diet by analysing diagnostic prey remains from the stomach contents of bycaught and beachcast individuals. I describe the prey species taken, quantify relative importance via estimation of prey size from fish otoliths and squid beaks, and investigate dietary differences between the two main Hector's dolphin populations on the South Island east and west coasts. The results are discussed in the context of prey availability, based upon current knowledge of prey assemblages available to Hector's dolphin. Hector's dolphin diet is then compared to the feeding ecology of the other *Cephalorhynchus* species.

2.2 METHODS

2.2.1 Sample collection

I analysed stomach contents from a total of 71 dolphins that had been bycaught and beachcast throughout New Zealand between 1984 and 2006. Location and date of the incident were recorded, along with body measurements, sex (when possible), and the extent of decomposition. Of the 71 stomachs and oesophagi examined for prey remains, four dolphins contained only eroded remains that could not provide accurate measurements. For another four, prey remains had degraded beyond use for species identification or measurement due to long-term storage in formalin or ethanol. Omission of these eight samples reduced the sample size suitable for quantitative analysis to 63 dolphins from the North Island west coast (*n*=2), and the South Island east (*n*=36), west (*n*=23) and south (*n*=2) coasts. Of these 63 dolphins, 79% were known to have been bycaught, and were found either entangled in nets or with significant net marks indicating entanglement as the cause of death. Markings on the remaining carcasses suggest the dolphins were bycaught and none are known to have stranded alive, which is a very rare occurrence for this species.

2.2.2 Stomach analysis

I washed the stomach contents through a 0.5 mm sieve and examined them for diagnostic prey remains, including fish otoliths, cephalopod beaks, crustacean exoskeletons, and remains of cartilaginous fish (e.g. teeth, spines). These were removed, air dried, and sorted by taxon. Otoliths and exoskeleton parts were stored in airtight plastic bags and beaks in 5% isopropyl alcohol solution. Prey remains were identified to genus or species if possible, by comparison with diagnostic remains for invertebrates and fish from the South Island continental shelf (Chris Lalas reference collection), and using the reference texts of Smale et al. (1995) and Furlani et al. (2007).

Remains were separated into left and right otoliths, upper and lower beaks, and those too eroded or broken to identify or measure. For fish, I calculated the minimum number of each species ingested as the total number of left or right otoliths (whichever was the greater) plus half the number of eroded otoliths. For cephalopods, I calculated the minimum number ingested as the total number of upper or lower beaks (whichever was the greater) plus half the number of broken beaks.

2.2.3 Data analysis

To estimate the original length and mass of prey items from their diagnostic remains I used power equations (Appendix: Table A1; A2), following Smale et al. (1995), calculated from a reference collection of whole fish, cephalopods, and crustaceans in collaboration with Dr Chris Lalas.

Prey remains from stomachs collected prior to 2002 were measured using digital callipers to the nearest 0.01 mm. Otolith length and width, and beak rostral length were recorded. Due to the small size and large quantity of otoliths in some samples, I digitally photographed and measured otolith remains gathered post 2002 using ImageJ software (Abramoff et al. 2004). To test the difference between the two measurement methods, a subsample of post 2002 otoliths from three species: ahuru (*Auchenoceros punctatus*), red cod (*Pseudophycis bachus*), and hoki (*Macruronus novaezelandiae*), were measured using both callipers and ImageJ software. These species were chosen as they provide a good representation of the range in size and shape of all otoliths examined. Otolith size results did not significantly differ between the two methods (paired *t*-test, t_{72}=1.355, P=0.180) and no measurement bias was found (r^2=0.98, P<0.001).

For each species in each sample, I used the left or right otolith measurements (whichever were the more numerous) as input in the equations to estimate the size of the prey. Similarly, squid size was estimated from the size of upper or lower squid beaks. In the case where both categories contained the same number of measured samples, I used the measurements for left otoliths and lower beaks in the power equations.

In order to mitigate biases associated with the analysis of digested prey remains, and avoid underestimating prey size (Jobling and Breiby 1986, Pierce and Boyle 1991), eroded otoliths were not measured. Eroded otoliths were allocated either the average size of conspecifics in the same stomach, or if no others were present, conspecifics across all stomach samples (e.g. Gannon and Waples 2004)

The relative importance of each species was estimated as %O (the percentage of stomachs examined containing that species), %N (the percentage of the total number of prey in all stomachs), and %M (the percentage of the total mass of prey in all stomachs). The total reconstructed mass of a prey species was calculated as the product of the number of prey items eaten and the average mass of that species. Each of these measures provides different information on the dolphins' feeding habits and the relative importance of prey species in their diet.

To assess sample size sufficiency in describing Hector's dolphin diet, I randomised the order of stomachs sampled 10,000 times, and plotted the cumulative number of species discovered as a function of stomach number (Ferry and Cailliet 1996, Cortés 1997).

2.2.4 Diet variability

My sample size allows for a comparison of diet between males (*n*=30) and females (*n*=27) from the two main populations; the South Island east coast (SIEC; *n*=35) and west coast (SIWC; *n*=22). Both factors were analysed in $R_{2.11.1}$ using the Scheirer-Ray-Hare (SRH) test, an extension of the Kruskal-Wallis test (Dytham 2011), with a sequential Bonferroni adjustment of α to minimize Type 1 errors (Rice 1989). Sample size was insufficient to compare diet across years, seasons or dolphin ages. The majority of samples (84%) were collected during spring and summer months.

Due to the large number of zeros typical of stomach content data, parametric testing using two-way ANOVA was not valid. The SRH test was used to compare both the number and mass of common prey consumed, as well as overall prey diversity, calculated using the Shannon-Weiner Diversity Index (H′) (Krebs 1989). I considered prey to be common when their occurrence was >25% for any group of the sample set.

Categorisation of prey species by habitat (Paulin et al. 2001) provides insight into where in the water column Hector's dolphins forage. Three habitat categories were defined as follows: Demersal: live and feed on or near the seafloor; Benthopelagic: live and feed at the seafloor and throughout the water column; Epipelagic: live and feed in surface waters. Occurrence of each prey type was examined for all stomachs collected, and compared between populations and sexes using the SRH test.

2.3 RESULTS

2.3.1 Overall diet composition

In total, I identified 22 fish, two cephalopod, and five crustacean species from the diagnostic remains of all 63 stomachs examined (Table 2.1). This equated to a minimum number of 4,460 prey items with a total reconstructed mass of 55,104 g. In terms of number and mass eaten, fish contributed most to the dolphins' diet (95% and 87% respectively), followed by cephalopods (3% and 13%) and crustaceans (1% and <1%).

Thirteen of the 22 prey species occurred in >10% of all the stomachs examined (Table 2.2), while only four; red cod, ahuru, arrow squid (*Nototodarus* sp.) and sprat (*Sprattus* sp.); were commonly eaten (>25% O).

Table 2.1: A list of all prey identified and their reconstructed mass and length. Data were collected from diagnostic remains from 63 stomach contents of Hector's dolphins bycaught and beachcast throughout New Zealand between 1985 and 2006.

			Mass (g)			**Length (cm)**		
Prey		***n***	**Mean ± SD**	**Min**	**Max**	**Mean± SD**	**Min**	**Max**
FISH								
Sardinops neopilchardus	Pilchard	9	24.6 ± 9.4	11	41	13.3 ± 1.7	11	16
Sprattus sp.	Sprat	86	12.1 ± 13.0	2	91	10.4 ± 2.1	7	19
Engraulis australis	Anchovy	29	4.0 ± 1.9	2	8	7.8 ± 1.2	6	10
Lampanyctodes hectoris	Hector's lanternfish	365	2.1 ± 0.9	0.7	7	5.9 ± 0.7	4	9
Auchenoceros punctatus	Ahuru	520	4.0 ± 3.8	0.1	20	8.3 ± 3.3	2	16
Pseudophycis bachus	Red cod	170	107.6 ± 135.6	0.1	830	17.9 ± 10.1	2	44
Macruronus novaezelandiae	Hoki	15	93.3 ± 63.8	2	266	28.9 ± 8.9	8	45
Merluccius australis	Hake	32	65.0 ± 64.6	4	313	20.0 ± 6.6	9	37
Coelorinchus aspercephalus	Oblique banded rattail	7	60.9 ± 33.3	16	104	23.1 ± 4.7	16	28
Lepidorhynchus denticulatus	Javelinfish	106	21.9 ± 28.1	0.1	162	18.6 ± 5.7	3	28
Paratrachichthys trailli	Common roughy	1	92.6	-	-	9.5	-	-
Nemadactylus macropterus	Tarakihi	15	12.4 ± 4.5	7	25	9.2 ± 1.0	8	12
Aldrichetta forsteri	Yelloweyed mullet	10	158.3 ± 107.3	20	302	21.0 ± 6.6	12	28
Notolabrus sp.	Wrasse	1	215.8	-	-	22.3	-	-
Crapatalus sp.	Stargazer	128	14.7 ± 25.1	0.8	128	10.2 ± 4.1	5	24
Forsterygion sp.	Triplefin	1	2.0	-	-	6.0	-	-
Grahamichthys radiata	Graham's gudgeon	160	0.5 ± 0.4	0.1	2	4.1 ± 0.6	3	6
Thyrsites atun	Barracouta	6	27.6 ± 14.9	3	44	18.2 ± 4.8	9	22
Seriolella brama	Blue warehou	4	28.2 ± 32.4	3	73	10.2 ± 4.5	6	16
Pelotretis flavilatus	Lemon sole	1	195.8	-	-	27.8	-	-
Peltorhamphus sp.	Sole	1258	5.4 ± 48.0	0.1	1282	4.4 ± 4.0	0.5	50
Rhombosolea sp.	Flounder	1	37.0	-	-	18.6	-	-
CEPHALOPOD								
Nototodarus sp.	Arrow squid	75	48.3 ± 118.9	0.1	960	17.1 ± 9.4	3	61
Sepioloidea pacifica	Pacific bobtail squid	4	4.3 ± 1.8	2	6	1.8 ± 0.2	2	2
CRUSTACEAN								
Pontophilus australis	Sand shrimp	1	0.4	-	-	3.6	-	-
Halicarcinus sp.	Pillbox crab	46	0.1 ± 0.1	0.1	0.7	0.6 ± 0.2	0.3	1
Macrophthalmus hirtipes	Mud crab	3	2.5 ± 0.6	2	3	1.9 ± 0.2	2	2
Nectocarcinus antarcticus	Red swimming crab	1	0.2	-	-	0.9	-	-
Ovalipes catharus	Paddle crab	4	3.6 ± 5.7	0.2	12	2.1 ± 1.3	1	4

Table 2.2: Composition of stomach contents from Hector's dolphins from the South Island east coast (SIEC), west coast (SIWC), south coast (SISC) and North Island west coast (NIWC). Diet composition is presented for male and female dolphins, and those of unknown sex, and is defined by three measures (%O / %N / %M): percentage by occurrence, number and mass. The symbol '+' is used to indicate <0.5%.

	All Samples	**SIEC**			**SIWC**			**SISC**	**NIWC**	
		Male	**Female**	**Unknown**	**Male**	**Female**	**Unknown**	**Female**	**Male**	**Female**
Prey	***n* = 63**	***n* = 19**	***n* = 16**	***n* = 1**	***n* = 11**	***n* = 11**	***n* = 1**	***n* = 2**	***n* = 1**	***n* = 1**
FISH										
Pilchard	3/+/1				18/1/5					
Sprat	25/8/7	26/20/16	19/4/2		45/5/7	18/+/+	100/56/63			
Anchovy	11/2/1		6/+/+		27/5/3	27/2/1				
Hector's lanternfish	14/21/3	11/8/1	6/3/+	100/96/73	27/24/9	18/31/5				
Ahuru	49/22/7	37/17/3	56/19/6		64/16/15	45/45/9	100/17/1		100/100/100	100/43/6
Red cod	59/4/37	79/4/39	63/8/60	100/3/21	27/+/1	36/6/42	100/7/17	100/17/27		100/40/7
Hoki	10/+/3	5/+/3			18/+/8	27/+/6				
Hake	13/1/4	16/1/1	6/1/3		27/1/19	9/+/3				
Oblique banded rattail	5/+/1	5/+/1	6/+/2			9/+/1				
Javelinfish	8/3/5				27/4/12	18/6/13				
Common roughy	2/+/+					9/+/1				
Tarakihi	3/1/1	5/2/2			9/1/1					
Yelloweyed mullet	14/+/3	26/+/9	13/+/2			9/+/+	100/7/5			
Wrasse	2/+/+	5/+/1								
Stargazer	21/5/6	21/6/9	38/21/11		9/+/1	18/1/1				
Triplefin	2/+/+	5/+/+								

	All Samples	SIEC			SIWC			SISC	NIWC	
		Male	**Female**	**Unknown**	**Male**	**Female**	**Unknown**	**Female**	**Male**	**Female**
Prey	***n*=63**	***n*=19**	***n*=16**	***n*=1**	***n*=11**	***n*=11**	***n*=1**	***n*=2**	***n*=1**	***n*=1**
FISH										
Graham's gudgeon	13/11/+	21/33/1	19/12/+		9/1/+					
Barracouta	3/+/+		6/1/1			9/+/+				
Blue warehou	6/+/+	5/+/1			9/+/+	18/1/+				
Lemon sole	2/+/+		6/+/1							
Sole	21/17/7		38/21/10		18/40/11	18/3/5	100/3/1	50/8/40		100/15/86
Flounder	2/+/+									100/2/1
CEPHALOPOD										
Arrow squid	37/3/13	26/4/12	26/6/1	100/1/6	36/1/7	55/3/12	100/10/13	100/75/33		
Pacific bobtail squid	6/+/+	5/+/+	19/1/+							
CRUSTACEAN										
Sand shrimp	2/+/+		6/+/+							
Pillbox crab	11/1/+	24/4/+	13/1/+		9/+/+					
Mud crab	3/+/+		13/+/+							
Red swimming crab	2/+/+	5/+/+								
Paddle crab	5/+/+	5/+/+	13/+/+							

Red cod and ahuru were the most frequently eaten prey, found in 59% and 49% of all stomachs respectively. Red cod, being a relatively large fish compared to ahuru, contributed little in terms of the number of fish eaten over all stomachs examined (4%, compared to 22% for ahuru), but made a high contribution in terms of mass (37% compared to 7% for ahuru). Arrow squid was the only other species contributing >10% in terms of mass, while Hector's lanternfish (*Lampanyctodes hectoris*, 21% N) and sole (*Peltorhamphus* sp., 17% N) were also eaten in relatively large numbers.

Stomachs of the six smallest Hector's dolphins analysed in this study contained milk but no prey remains. These dolphins (6 females, 1 male) were 77-90 cm standard length (SL: snout tip to tail notch). The next largest dolphin, measuring 99 cm SL (female), contained milk and arrow squid prey remains. Milk was not found in stomachs of any dolphins larger than 107 cm.

Only three items, two crab naupilii (length *ca.* 0.5 cm) and one parasitic isopod (length *ca.* 1 cm), were inconsistent with direct capture by dolphins and I did not include these in analyses. One stomach contained only fresh and intact Graham's gudgeon (*Grahamichthys radiata*) measuring 3.0-5.6 cm. This verified that very small fish are taken directly by Hector's dolphins. None of the species and size mixtures in any stomachs were compatible with smaller items being derived from the stomach contents of larger prey.

Figure 2.1 indicates that when sampled in random order, the first 30 stomachs examined accumulate on average 24 of the 29 prey species. Overall, the samples appear to be approaching an asymptote.

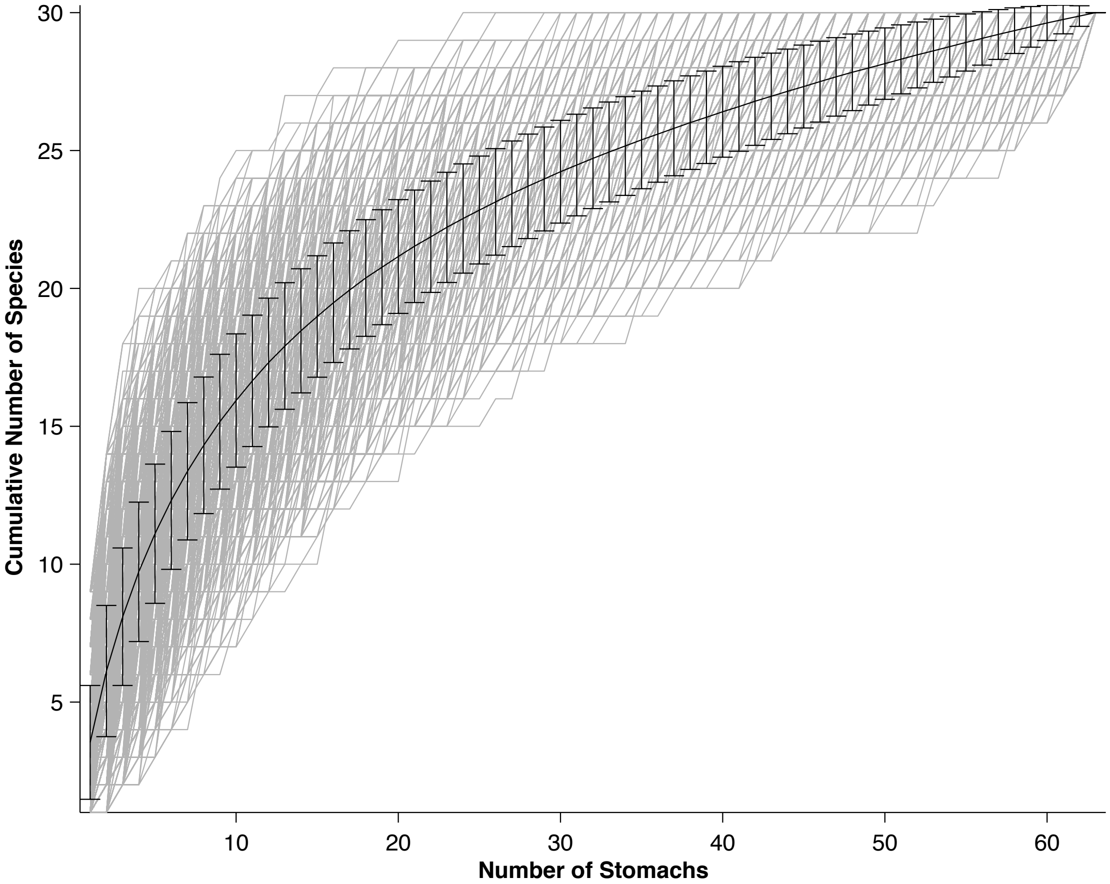

Figure 2.1: The cumulative number of species discovered as a function of stomach number for 10,000 randomized selections of the stomachs examined (shown in grey). The black line indicates the mean cumulative number of species ± standard deviation.

2.3.2 Length distribution

Reconstructed prey lengths show that Hector's dolphins consume prey ranging from less than 1 cm to greater than 60 cm in total length (Figure 2.2).

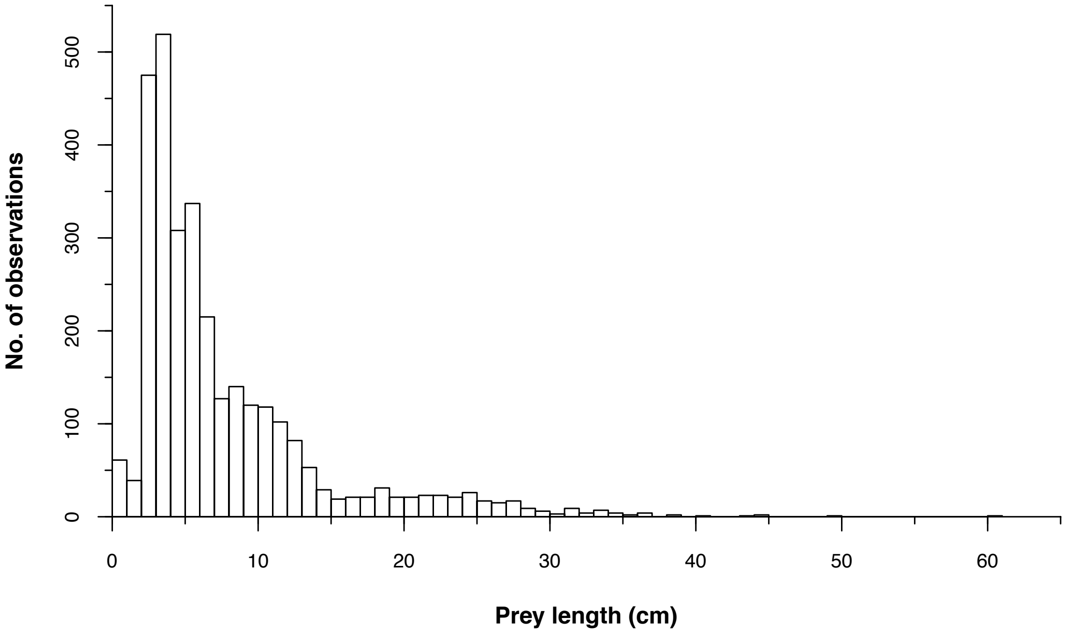

Figure 2.2: Length distribution of prey consumed by Hector's dolphins throughout New Zealand, combined across all stomachs examined (*n*=63).

The distribution of prey size is highly skewed, with over 75% of the prey items measuring less than 10 cm (Figure 2.2). Prey consistently larger than 10 cm were pilchard (*Sardinops neopilchardus*), yelloweyed mullet (*Aldrichetta forsteri*) and rattail (*Coelorinchus aspercephalus*), from which only a small number of otoliths were available for measurement (*n*=9, 10, 7 respectively). The largest prey item found was a 60.8 cm long arrow squid, far above the mean length for this species in this study (17.1 cm total length; Table 2.1).

2.3.3 Diet variability

SIEC samples contained a total of 25 prey species (18 fish, two cephalopod, and five crustacean) from 36 stomach samples (Table 2.2). A minimum number of 2,024 prey items were eaten, with a total reconstructed mass of 29,491 g. Overall, commonly consumed prey (>25% O) were ahuru, red cod and arrow squid. Sprat and yelloweyed mullet were found in 26% of male stomachs while 38% of females had consumed stargazer (*Crapatalus* sp.) and sole. Red cod contributed most to prey mass, particularly for females, while Graham's gudgeon, sprat, stargazer, sole, and ahuru were eaten in large numbers.

SIWC samples contained a total of 20 prey species (18 fish, one cephalopod, and one crustacean) from 23 stomach samples (Table 2.2). This equated to a minimum number of 2,363 prey items, with a total reconstructed mass of 20,513 g. On the west coast, other species commonly consumed were anchovy (*Engraulis australis*), Hector's lanternfish, hake (*Merluccius australis*), hoki and javelinfish (*Lepidorhynchus denticulatus*). Only red cod contributed substantially to the mass of prey, while large numbers of ahuru, sole, and Hector's lanternfish were eaten.

All comparisons revealed no significant interaction between population and sex (SRH test, P>0.05) so these factors can be examined independently. A significantly greater number and mass of javelinfish were eaten on the SIWC than the SIEC (H_1=8.566, P=0.003; H_1=8.543, P=0.003, respectively). SIWC dolphins also consumed a significantly greater number of anchovy (H_1=9.658, P=0.002). No significant differences were found between sexes with sequential Bonferroni correction.

Prey diversity (H′) varied from 0, for stomachs containing only one prey species, to 1.66. On average, SIEC dolphins had higher prey diversity (H′=0.60) than those from the SIWC (H′=0.55). Female prey diversity (H′=0.60) was slightly higher than the average for males (H′=0.57). None of these comparisons was statistically significant (SRH test, P>0.05).

Both demersal and benthopelagic prey species were found in a high percentage of all stomachs examined (Figure 2.3). Comparisons of the number of prey species consumed from each habitat indicated no significant interaction between population and sex, and no significant effect of sex (SRH test, P>0.05). SIEC and SIWC dolphins were found to forage to a different extent in each habitat, however. As indicated by Figure 3, significantly more benthopelagic and epipelagic species were eaten on the west coast (H_1=5.708, P=0.017; H_1=8.487, P=0.004, respectively), while SIEC dolphins consumed a greater number of demersal species (H_1=11.332, P=0.001).

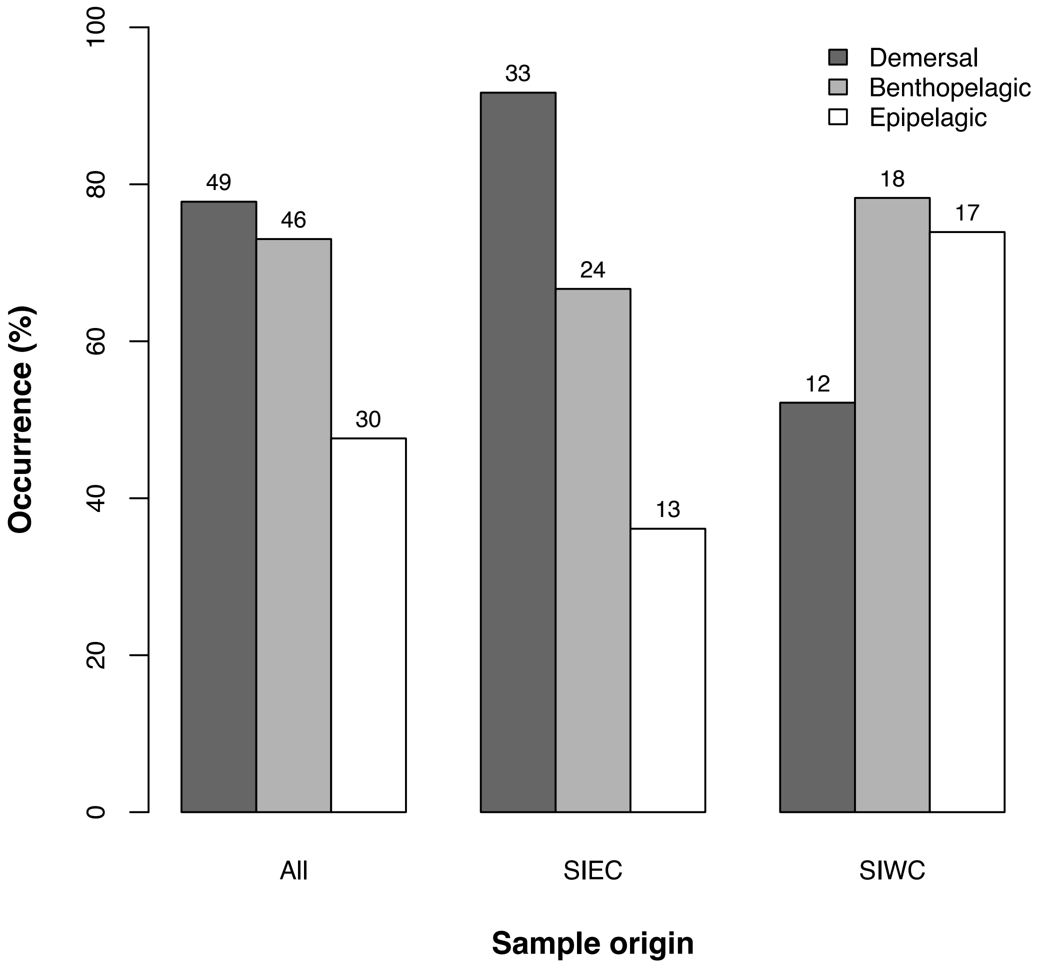

Figure 2.3: Occurrence (%) of prey types in all stomachs examined (*n*=63), and those collected from the South Island east coast (SIEC; *n*=36) and west coast (SIWC; *n*=23). Numbers above each bar indicate absolute occurrence (the number of stomachs containing each prey type).

2.4 DISCUSSION

2.4.1 Dietary composition and prey distribution

Hector's dolphins eat a wide-variety of prey species, with a total of 29 identified from the 63 stomachs examined. The rate of species discovery suggests that while the analysis of additional stomachs may reveal new prey species, the current sample represents the diet of Hector's dolphins fairly well. While a broad range of species were eaten, only a few were common and contributed substantially to the dolphins' diet. Overall, the two prey species with the greatest contribution were red cod and ahuru. These prey were the most commonly consumed and contributed most in terms of mass and number respectively.

Hector's dolphins evidently forage throughout the water column. The prey species identified in this study come from a wide range of habitats. I frequently found both epipelagic prey and those living near the seafloor in the stomachs examined, but overall, demersal and benthopelagic prey were most prevalent. This is consistent with incidental observations of foraging behaviour made during long-term photo-ID studies of Hector's dolphins at Banks Peninsula. Surface feeding is not common, but has been observed throughout the year, in a range of water depths from 2-25 m, on small fish including sprat, pilchard, and yelloweyed mullet. White-fronted terns (*Sterna striata*) are often seen diving in an apparent commensal association with surface-feeding dolphins, likely due to increased accessibility of prey (Bräger 1998). Feeding at depth is not directly observable, but is assumed to be the main activity during "long-diving" in which dolphins dive for up to *ca*. 90 s (Slooten and Dawson 1994). Hector's dolphins have been observed following inshore trawlers in large groups in water 9-32 m deep (Rayment and Webster 2009), and are likely to be taking fish stirred up, but not caught by the trawl net. The trawl net and steeply descending traces consistent with dolphins diving to the seafloor around the net are regularly observed on the echosounder during these occasions.

I found significant differences between the diets of dolphins from the South Island east and west coasts. One contributing factor to these differences was the presence of javelinfish in several west coast individuals. This species did not occur in samples from other regions. All five stomachs containing this species were collected near Haast in southern Westland, where deep water can be found close to shore. In this region, the 100 m and 500 m depth contours lie only approximately 5 and 9 nautical miles (n.mi.) from shore respectively. This contrasts with the wide continental shelf around Banks Peninsula on the east coast, where water is less than 100 m deep out to 20 n.mi. from shore. Adult javelinfish have been found most commonly in water 80-450 m deep (e.g. Last et al. 1983), but have also been recorded from as shallow as 60 m depth in Australian waters (Gomon et al. 1994).

Many fish surveys are carried out well beyond the typical extent of Hector's dolphin distribution, but available inshore data does provide some information on the assemblages present in Hector's dolphin habitat. Research trawls on the SIEC continental shelf and upper slope (10-400 m depth) have found two of the identified prey species; red cod and barracouta (*Thyrsites atun*) to be among the three most abundantly caught demersal fish, along with spiny dogfish (*Squalus acanthias*) (Beentjes et al. 2002). The characteristic teeth and dorsal fin spines of spiny dogfish were not present in our samples, so there is no indication that this species is eaten. During these trawls, several other prey species were also found to be among the most abundant in water <100 m deep, including tarakihi (*Nemadactylus macropterus*), sole, lemon sole (*Pelotretis flavilatus*), arrow squid and rattails (Beentjes et al. 2002). In these fish surveys, cod-end mesh size varied from 7.4 cm in winter surveys to 2.8 cm in the summer. The majority of red cod measured around 35 cm length, though individuals <20 cm were also caught. Tarakihi size peaked at 13-18 cm and arrow squid matched the size distribution of those eaten by Hector's dolphins well, with peaks at 10, 21 and 30 cm mantle length (Beentjes and Stevenson 2000).

Research trawl surveys on the SIWC in water 20-400 m deep (Stevenson and Hanchet 2010) found spiny dogfish, red cod, barracouta and silver dory (*Cyttus novaezealandiae)* to make up over 51% of the total catch by weight. Arrow squid (*N. sloanii*), barracouta and spiny dogfish occurred in over 90% of the tows. Tows shallower than 200 m caught 95% of the red cod biomass, with the highest catches between 25 and 100 m. In these surveys, a 6 cm cod-end mesh size was used. Again, relatively few captured red cod were smaller than 20 cm in length. Tarakihi were mainly >25 cm long, with >62% biomass caught between 100-200 m deep. Captured hoki were mainly 17-26 cm long.

Despite extensive surveys, Hector's dolphins are very rarely seen in water deeper than 90 m on the SIEC (e.g. Rayment et al. 2010) and 60 m on the SIWC (e.g. Rayment et al. 2011). Trawl surveys often do not cover the close inshore habitat <20 m deep where Hector's dolphins are most often encountered, especially in summer (Rayment et al. 2010). It is likely that many of the very small prey eaten by the dolphins (both juveniles of larger prey species such as red cod, and adults of smaller species such as triplefins (*Forsterygion* sp.)) are captured in these areas, particularly in bays and harbours. For example, in a study of fish species within a tidal flat of the Manukau Harbour, Morrison et al. (2002) observed several Hector's prey species, including yelloweyed mullet, sole, flounder (*Rhombosolea plebeia*), anchovy and Pacific bobtail squid (*Sepioloidea pacifica*). Most individuals they caught measured <10 cm long.

Hector's dolphins consumed prey up to 60.8 cm in total length, but the majority of prey measured <10 cm. Some species found in the stomach contents, including javelinfish and hake, are generally thought of as mid- to deep-water species, but it appears that Hector's dolphins are preying upon juvenile individuals, which range into shallower water. Hake adults for example, commonly occur in areas deeper than 350 m (Hurst et al. 2000), but immature individuals 25-40 cm long are widespread in water shallower than 100 m around the South Island (Patchell 1981). Juvenile red cod have been caught around New Zealand, mostly in water shallower than 250 m (Hurst et al. 2000). Tarakihi juveniles have been caught in bottom trawls mainly off the SIEC in water depth <100 m (Hurst et al. 2000), and are thought to be abundant in many rocky inshore areas, not available to trawl sampling (Annala 1987). Juvenile *N. gouldi* squid have been found mainly between the North Taranaki Bight and Westland <200 m deep, while *N. sloani* are distributed inshore to the east and south of the South Island (Hurst et al. 2000). Adult sole and flounder have been caught in research trawls mainly in <100 m of water (Anderson et al. 1998) while juveniles occur close inshore and seasonally use estuaries and harbours as nurseries (e.g. Roper and Jillett 1981)). Young blue warehou (*Seriolella brama*) are often found in small schools in harbours and bays (Ayling and Cox 1982) while adults range deeper out to 400 m (Hurst et al. 2000).

Hector's lanternfish were eaten by the dolphins in relatively large numbers. This species is considered to be one of the shallowest living myctophids, and is common over shelf and slope waters (Robertson 1977). The occurrence of lanternfish in Hector's dolphin stomachs suggests that some individuals of this fish species occur in shallow water. Lanternfish adults are frequently associated with the deep scattering layer, rising from deeper water to the surface at night, but current knowledge of Hector's dolphin movements indicates no evidence of foraging in such areas. Extensive visual observations during daylight hours indicate that the dolphins inhabit inshore waters shallower than *ca.* 90 m deep (e.g. Rayment et al. 2010). Day and night acoustic surveys of dolphin density at Banks Peninsula have found no evidence of diel variation in movements (Rayment et al. 2009a) and so it is unlikely that the dolphins gain access to prey such as lanternfish by moving out over deeper offshore water at night.

Several fish species have been found to increase in density inshore, in areas 30-100 m deep during the summer, with lower densities recorded in winter. Trawl surveys on the SIEC have found this to be the case for several Hector's prey species including red cod, barracouta, rattails and tarakihi (Beentjes et al. 2002). As well as using protected inshore areas as nurseries, these patterns are possibly linked to movements of food sources. Red cod, for example, are known to feed extensively on squat lobster (*Munida gregaria*) during summer and autumn, which occur in large shoals throughout inshore waters and harbours during that time (Carter and Malcolm 1926). The habitat preferences of marine mammals are similarly assumed linked to prey to some degree (e.g. reviewed by Stevick et al. 2002).

Cooperative feeding such as herding or corralling of prey has only rarely been observed for Hector's dolphins, though it has been described for related species, including Commerson's (Goodall et al. 1988) and Chilean dolphins (Heinrich 2006). Such behaviour is often linked to the abundance of schooling prey in the region. When prey is more patchily distributed or less abundant, dolphins are more likely to forage individually (Würsig 1986).

Overall, our knowledge of Hector's dolphin diet and distribution suggests that these predators primarily consume small and often juvenile prey, the distribution of which corresponds to the dolphins' close proximity to shore, particularly in the summer months. Prey consumption appears to reflect species availability, which differs between the South Island east and west coasts, likely due in part to the bathymetric differences between these two regions.

2.4.2 Comparison with other species

Seasonal changes in distribution, potentially related to prey movements have also been reported for other small cetaceans including Chilean dolphin (Heinrich 2006) and Commerson's dolphin (Goodall 1988). Like most aspects of their biology, the diets of the other *Cephalorhynchus* species are less well-known than that of Hector's dolphin. It appears the diets are broadly similar however, as all species are reported to feed throughout the water column on demersal and pelagic prey, with both fish and cephalopods making a large dietary contribution. There are also similarities in the size of prey eaten, as juveniles appear to be targeted. All members of the genus have a coastal distribution, occurring primarily in waters shallower than 150 m (Dawson 2009) and so their diets of juvenile coastal species reflect their habitat preferences.

Like Hector's dolphins, Chilean dolphins have been observed surface feeding in association with terns, as well as long-diving (Ribeiro et al. 2007). Dietary information for this species comes from a small sample of twenty individuals, and little quantitative information has been reported. Known prey include pelagic species: Anchovetas (*Engraulis ringens*), Chilean jack mackerel, (*Trachurus murphyi*) and herring (*Clupea bentincki*); as well as species associated with the seafloor: drum (*Cilus gilberti*), Patagonian blenny (*Eleginops maclovinus*) and Patagonian squid (*Loligo gahi*) (Torres et al. 1992). Patagonian squid were found in 30% of stomach contents examined. Several of these prey species inhabit estuaries and sheltered bays, especially in spring and summer.

From the stomach analysis of nine Commerson's dolphins in the San Jorge Gulf (Crespo et al. 1997), the most important prey were found to be juvenile hake (*Merluccius hubbsi*) and shortfin squid (*Illex argentinus*). Other species include Patagonian squid, bobtail squid (*Semirossia tenera*), anchovy (*Engraulis anchoita*), butterfish (*Stromateus brasiliensis*) and southern cod (*Patagonotothen ramsayi*). Hake consumed were *ca*. 10 cm long; smaller than those caught in a nearby fishery. Off Tierra del Fuego, the main prey were sprat (*Sprattus fuegensis*), hoki (*Macruronus magellanicus*), Patagonian squid, southern cod and silverside (*Austroatherina* sp.) (Bastida et al. 1988). Iñíguez and Tossenberger (2007) observed Commerson's dolphins surface feeding on silverside, often herding the fish against anchored ships and piers, and close to kelp forests.

Sekiguchi et al. (1992) examined 21 stomach contents of Heaviside's dolphin, collected from stranded and bycaught individuals between 1969 and 1990. Overall, five cephalopod and 12 fish species were identified. Demersal prey, particularly hake and *Octopus* sp. contributed the most, though pelagic prey including goby

(*Sufflogobius bibarbatus*) were also present. The hake and goby consumed were mainly juveniles, averaging 19.5 cm and 5.3 cm in length respectively.

2.4.3 Interactions with fisheries

There is no indication that Hector's dolphins scavenge fish from gillnets. Hickford et al. (1997) examined the size selectivity of mesh sizes commonly used by some commercial gill net fishers in New Zealand. They found that 3.5 inch mesh catch peaked at 25 and 40 cm fork length, while 4.5 and 5.5 inch mesh mostly caught fish of 35 and 50 cm fork length. These sizes are well above the typical length of Hector's dolphin prey. Hector's dolphins are most often caught in inshore gillnet fisheries targeting rig (*Mustelus lenticulatus*), elephant fish (*Callorhyncus milii*) and school shark (*Galeorhinus galeus*) (Dawson 1991a). These nets typically have larger mesh sizes (6.5-7 inches, up to 9 inches for school shark) than tested by Hickford et al. (1997), hence are even less likely to catch fish small enough for Hector's dolphins to eat.

It is more likely that Hector's dolphins are susceptible to gillnet entanglement because they feed throughout the water column, not only in surface waters but on the seafloor, and because their diet is similar to that of the targeted catch species. School sharks, for example, are known to feed on barracouta, anchovy, cod, crustaceans, small cephalopods, and demersal reef fish (Olsen 1954). Similar overlap in food sources is indicated for target species in the Gulf of Maine gillnet fishery and harbour porpoise (Gannon et al. 1998), a species also very susceptible to gillnet entanglement (Read and Gaskin 1988). Spatial overlap between commercially targeted Chondrichtyhans and Hector's dolphins is greatest in summer, when rig, elephant fish and school shark are all well known to aggregate in inshore coastal waters (Francis 1998).

Of the main prey species, red cod is also important to both commercial and recreational fishermen. Over the course of this study, this species has been a key target species in the Southern Inshore Trawl Finfish Fishery (MFish 2007), and biomass trends have shown a substantial decline since the mid-1990s (MFish 2011). Red cod recruitment varies considerably between years, however the length and magnitude of decline in commercial and recreational catch indicate that fishing pressure may also be responsible for the decreased abundance (MFish 2007). This is particularly the case on the SIEC, including Banks Peninsula, a stronghold for Hector's dolphins. This region has been important for recreational fishing of red cod in the past, but recently, local fishermen have found that what used to be one of the most abundant species is now relatively uncommon catch (MFish 2007). As this study has shown red cod to contribute most in terms of mass to Hector's dolphin diet, this raises concern. Dietary analyses should continue in the future to assess whether decreased red cod availability is reflected in the current diet.

2.4.4 Limitations of this method

Stomach content analysis has inherent biases, which have been discussed extensively in the literature (e.g. reviewed by Pierce and Boyle 1991). In this study, one potential limitation comes from the fact that my samples were not randomly gathered, but came from individuals found beachcast or recovered dead from gillnets. Sampling is therefore somewhat opportunistic, and so sample size is limited. Small sample sizes can lead to single individuals having a high influence on overall results. In this study for example, four of the five dolphins containing javelinfish remains were found entangled in the same net and so are potentially not representative of the west coast population as a whole.

Stomach content analysis only provides information on what has been recently ingested; the method does not take into account the different digestibility of prey items. This could lead to some prey species being more easily detected than others. Some prey remains, for example cephalopod beaks, may be retained in stomachs for long periods (Pitcher 1980), and prey with no hard parts or with cartilaginous skeletons are likely to be underestimated (Pierce and Boyle 1991). Partially digested otoliths could lead to an underestimation of original prey size (Jobling and Breiby 1986), which is why I did not measure eroded otoliths. Some prey remains may also be lost due to regurgitation; a few individuals in this study had prey remains in the oesophagus.

Conclusion

This study presents the first quantitative analysis of Hector's dolphin diet, based on detailed analysis of stomach contents from 63 dolphins. The results indicate that Hector's dolphins take a wide variety of prey throughout the water column, but that their diet is dominated by a few demersal and mid-water species. Small and juvenile prey are targeted, the movements of which appear to reflect Hector's dolphins' coastal distribution. Comparable diets have been reported for related species with similar habitat preferences. Knowledge of Hector's dolphin diet may assist in interpreting habitat preferences and behavioural patterns. Using this as a baseline, further research can aim to determine how prey availability influences Hector's dolphin movements, and could identify which habitats have the greatest potential for future population recovery of this endangered species.

CHAPTER 3

YOU ARE WHAT YOU EAT: STABLE ISOTOPE ANALYSIS OF HECTOR'S DOLPHINS AND THEIR PREY

3.1 INTRODUCTION

In a chemical demonstration of 'you are what you eat', the stable isotope signatures of consumers largely reflect those of their prey (DeNiro and Epstein 1978, 1981). Stable isotope analysis has thus become a popular approach to studying diet (Kelly 2000, Crawford et al. 2008), and can be an especially useful tool in studies of species such as marine mammals (Newsome et al. 2010), whose foraging habits are difficult to observe.

Previous work based upon stomach contents (Chapter 2; Miller et al. 2013), found Hector's dolphin diet to be similar to that of other *Cephalorhynchus* species. Hector's dolphins were found to feed throughout the water column, with the majority of prey items measuring <10 cm in length. While a total of 29 prey species were identified, their diet was dominated by a few demersal and mid-water species. Red cod (*Pseudophycis bachus*) contributed most in terms of mass, and ahuru (*Auchenoceros punctatus*) and Hector's lanternfish (*Lampanyctodes hectoris*) were consumed in large numbers. Dietary methods such as this, which study prey remains, have inherent biases, however (Pierce and Boyle 1991). One substantial limitation is that they only provide dietary information on what has recently been ingested. As Hector's dolphins are typically bycaught and beachcast during spring and summer months (Dawson 1991a), the majority of stomach samples are collected opportunistically at this time, leading to a seasonal bias. Insights into long-term feeding habits are needed to gain more representative picture of Hector's dolphin diet.

Stable isotope analysis, introduced in Chapter 1, has been used in previous studies of cetaceans (e.g. Di Beneditto et al. 2011, Mèndez-Fernandez et al. 2012) as an effective complementary method to traditional diet analyses. The recent development of isotopic mixing models (Phillips and Gregg 2003, Moore and Semmens 2008, Parnell et al. 2010, Phillips et al. 2014) has allowed this chemical analysis to provide quantitative data on diet composition and relative prey contribution. It is based upon the reliable and predictable isotope transformations during diet, which result in stable isotope signatures of predators reflecting those of their prey (DeNiro and Epstein 1978, 1981, Tieszen et al. 1983, Peterson and Fry 1987). Stable isotope signatures integrate diet on a timescale of months to years, depending upon the tissue examined (Tieszen et al. 1983), and can therefore serve as long-term indicators of trophic relationships. As stable isotope analysis cannot identify which prey were consumed without some prior knowledge of potential prey species to include in mixing models (Lesage et al. 2001), it is best used when complementing previous or concurrent diet studies, such as stomach content analysis.

In this study, I use stable isotope analysis in combination with the analysis of stomach contents (Chapter 2; Miller et al. 2013), to examine the foraging ecology of Hector's dolphin. In this chapter, I present analyses from a range of prey items and model their relative contribution to the dolphins' diet. This provides information on dietary preferences over a broader timescale, and resolves some of the biases inherent in stomach content analysis.

This work focuses on the diet of dolphins from the South Island east coast, because this area has the greatest sample size. In 1988 the Banks Peninsula Marine Mammal Sanctuary (BPMMS) was established between the Rakaia River and Sumner Head out to four nautical miles offshore (Dawson and Slooten 1993). Within these boundaries, commercial gillnetting was prohibited and recreational gillnetting seasonally restricted. This area supports the second largest regional population of Hector's dolphins (Dawson et al. 2004), and as part of this study I investigate whether there is evidence of a change in the dolphins' diet with respect to the creation of the BPMMS and the subsequent change in fishing activity.

3.2 METHODS

3.2.1 Sample collection

I sampled 42 Hector's dolphins, bycaught in gillnets or found beachcast along the South Island east coast between 1973 and 2010, from the Te Papa Museum and Massey University collections (Table 3.1). As only skeletal remains were available for the majority of these individuals, my analyses focused on bone collagen. Due to its slow metabolic rate, this tissue provides dietary information over a timescale of several years to decades for medium to large sized animals (Chisholm et al. 1982; Tieszen et al. 1983; Dalerum et al. 2005). Results will therefore represent a long-term average diet compared to the recently ingested prey remains recovered from stomach contents (Chapter 2; Miller et al. 2013). Permits from the Department of Conservation and Te Papa Museum allowed collection of small samples (a few mg) of bone from the rib cage of each dolphin.

When possible, I also collected muscle samples to allow comparison of the signatures of muscle and bone collagen and determine which enrichment values to use in the mixing model. As explained in Section 1.2.3, the best estimate of fractionation available for this study is that reported from controlled feeding experiments of pinnipeds (Hobson et al. 1996), and is for muscle tissue. I used the nine Hector's dolphins for which both muscle and bone samples were available to develop a relationship between the two, and hence predict muscle $\delta^{13}C$ & $\delta^{15}N$ ratios for the dolphins for which only bone samples were available. Muscle tissue has a higher turnover rate than bone collagen and provides dietary information over a timescale of weeks to months (Tieszen et al. 1983).

To examine the contribution of different prey to the dolphins' diet I needed to sample the isotope signatures of prey species. Samples were collected from species previously identified from Hector's dolphin stomachs, and from species that are common on the South Island east coast and within the size range taken by Hector's dolphins (up to 60 cm, but typically <30 cm length). Overall, I sampled 90 individual prey items comprising 15 fish species, one cephalopod and three crustacean species (Table 3.2). Prey items were caught between 2008 and 2012 during fieldwork at

Banks Peninsula or by local fishermen trawling in Banks Peninsula coastal waters. Animals collected were humanely euthanised (Ethics approval No. ET15/09). To maximise consistency, I sampled small pieces of muscle tissue from between the dorsal fin and lateral line of each fish, the legs and body of crabs and the mantle of arrow squid.

All dolphin and prey muscle samples were washed thoroughly with distilled water, bagged and labelled, then frozen at -20°C until prepared for stable isotope analysis.

3.2.2 Sample preparation

Bone collagen was extracted from the bone samples at GNS Science, Lower Hutt. Clean bone was demineralized with 0.5 M HCl until carbonates dissolved. The rough collagen matrix was then rinsed and converted to gelatin in a sealed tube with 0.01 M HCl, in an inert atmosphere at 100°C for 16 hours. The gelatin was then filtered through a 0.45 micron Acrodisc filter and freeze dried.

Muscle tissue was dried at 60°C then ground to a fine powder to homogenise the tissue. Lipid extraction was then carried out at the NIWA (National Institute of Water and Atmosphere) Hamilton laboratory on a DIONEX 200 accelerated solvent system (ASE). Differences in the lipid content of samples can confound the interpretation of $\delta^{13}C$ isotope ratios due to lipids being depleted in ^{13}C relative to protein and carbohydrate (Rounick and Winterbourn 1986). Recent studies have shown that lipid $\delta^{13}C$ values can differ by as much as 3-8‰ (Jardine and Cunjak 2006, Logan and Lutcavage 2006). As the proportion of lipid in muscle samples can vary between individuals, and is not easy to correct for after stable isotope analysis, it is generally preferred to extract lipids from each sample before analysis (Ricca et al. 2007).

During lipid extraction, the dried, homogenised samples were sub-sampled, wrapped in GF/C filters, secured with a staple and then uniquely labelled. The samples were then transferred to 22 mL s/s ASE cells and extracted three times with dichloromethane at 70ºC and 1500psi for a static hold time of 5 minutes. Traces of solvent were evaporated overnight in a 40ºC oven and the samples were stored in a desiccator until weighing for isotope analysis.

3.2.3 Stable isotope analysis

All carbon and nitrogen analyses were carried out at the NIWA stable isotope laboratory in Wellington on a Delta^{Plus} (Thermo-Finnigan, Bremen, Germany) continuous flow, isotope ratio mass spectrometer.

Between 0.6 and 0.8 mg of each dried sample was weighed into individual tin cups and sealed for stable isotope analysis. Samples were combusted in an NA 1500N (Fisons Instruments, Rodano, Italy) elemental analyser combustion furnace at 1020°C in a flow of oxygen and helium carrier gas. Oxides of nitrogen were converted to N_2 gas in a reduction furnace at 640°C. N_2 and CO_2 gases were separated on a Porapak Q gas chromatograph column before being introduced to the mass spectrometer detector via an open split Conflo II interface (Thermo-Finnigan, Bremen, Germany).

For every sample analysed, CO_2 and N_2 reference gas standards were introduced to the mass spectrometer. ISODAT (Thermo-Finnigan) software was used to calculate $\delta^{15}N$ against atmospheric air, and $\delta^{13}C$ against the CO_2 reference gas relative to PDB, correcting for ^{17}O. At the start of each run, % C and % N values were calculated relative to a laboratory reference standard of DL-Leucine (DL-2-Amino-4-methylpentanoic acid, $C_6H_{13}NO_2$, Lot 127H1084, Sigma, Australia). National Institute of Standards and Technology (NIST) standards were routinely used to check all internal standards. Repeat analysis of NIST standards produces data accurate to within 0.2 ‰, and a precision of better than 0.2 ‰, for both $\delta^{15}N$ and $\delta^{13}C$.

3.2.4 Data analysis

Predator

I performed all statistical analyses in R 2.14.2 (R Development Core Team 2012). I calculated 95% confidence intervals for the difference between means (Gardner and Altman 1986, Nakagawa and Cuthill 2007). If the confidence interval for a difference contained 0, the data were consistent with no “significant” difference between the two means. Differences in $\delta^{13}C$ & $\delta^{15}N$ bone collagen signatures between male (n=19) and female (n=21) dolphins were analysed, excluding results from two individuals whose sex was unknown.

To examine any effect of the BPMMS on Hector's dolphin diet, dolphin signatures were compared based upon the year and general location at which dolphins were recovered. Hector's dolphins have small alongshore home ranges (~50 km; Bräger et al. 2002, Rayment et al. 2009b) and so I assume that the location where an individual was found bycaught or beachcast was close to where it was resident.

Two factors and the interaction between them were considered: *Year* (whether the dolphin was collected 'before' (pre-1988) or 'after' (post-2006) the Sanctuary's creation in 1988) and *Area* (whether the dolphin was collected 'inside' or 'outside' of the Banks Peninsula Sanctuary). Those dolphins found within 60 km of the Sanctuary boundaries were classed as 'inside', while those 'outside' were collected from Timaru and Kaikoura, approximately 170 km to the south and north of Banks Peninsula respectively (Figure 3.1).

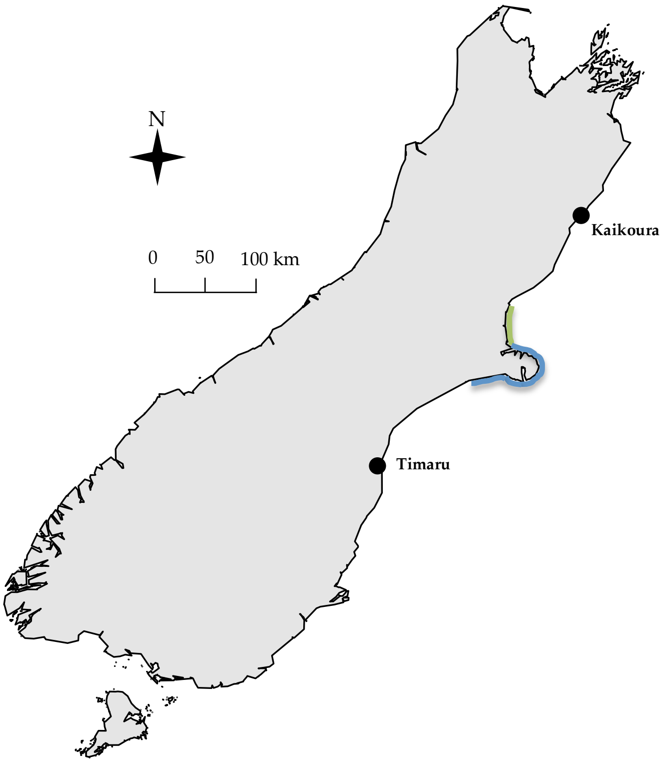

Figure 3.1: Map of the South Island of NZ indicating the regions from where dolphin samples were collected. The blue line outlines the location of the Banks Peninsula Marine Mammal Sanctuary (1988-2008). The green line outlines the northern boundary extension implemented in 2008.

Two-way ANOVA was used to examine the change in dolphin $\delta^{13}C$ & $\delta^{15}N$ signatures over time both inside and outside of the Sanctuary. The interaction between these two factors determined whether temporal changes in diet occurred solely within the Banks Peninsula area (thus likely connected to the creation of the BPMMS), or throughout all three regions sampled along the South Island east coast.

Prey

To estimate the relative contribution of prey to a predator's diet, prey signatures are required to be isotopically distinct. In order to determine the most distinct groupings within my data, three grouping methods were examined. Firstly, I categorised prey species into habitat groups according to Paulin et al. (2001). Four habitat categories were defined as follows - *Demersal*: live and feed on or near the seafloor; *Reef associated*: demersal fish that are closely associated with rocky reef habitat; *Benthopelagic*: live and feed at the seafloor and throughout the water column; *Epipelagic*: live and feed in surface waters. I then categorised the prey into four broad taxonomic groups: *Bony fish*, *Cartilaginous fish*, *Crustaceans* and *Cephalopods*. Cluster analysis (Ward's method) was then performed on the mean $\delta^{13}C$ & $\delta^{15}N$ signatures of each species to indicate any natural groupings in the data.

Discriminant analyses were then carried out on individual prey items to examine how successfully each prey sample could be assigned to its designated group. The assumptions of normality and homogeneity of variances were met in all analyses.

Diet analysis

I used the Stable Isotope Analysis in R (SIAR) package (Parnell et al. 2010) to estimate the proportional contribution of potential prey groups to the signatures observed in the dolphins. SIAR is a popular Bayesian isotopic mixing model fit via Markov chain Monte Carlo (MCMC) methods. SIAR produces simulations of plausible proportions of prey in the dolphins' diet consistent with the data. The probability density function distributions report the most probable allocation of diet sources and allows estimation of upper and lower credibility intervals (Parnell et al. 2010). The MCMC implementations were run for 500,000 iterations, with the first 50,000 iterations discarded.

3.3 RESULTS

3.3.1 Tissues

Comparison of muscle and bone collagen from nine Hector's dolphins revealed that on average, δ^{13}C was 2.94‰ (95% CI: 2.66 to 3.22‰) lower in the muscle samples than the bone collagen and did significantly differ between the two tissues. There was however, no evidence of a significant difference in δ^{15}N between the tissues (mean difference: -0.21‰; 95% CI: -0.47 to 0.06‰).

A moderate correlation was found between the δ^{13}C signatures of the bone collagen and muscle samples (t_7=2.855, P=0.025, R^2=0.472), while there was a strong correlation in δ^{15}N (t_7=5.286, P=0.001, R^2=0.771). From these results, I estimated the isotope signature of the muscle tissue for the remaining 33 dolphins using the known signature of their bone collagen samples, as shown in the following equations:

$$\delta^{13}\mathrm{C}_{Muscle} = 0.815 * \delta^{13}\mathrm{C}_{Bone} - 5.408$$

$$\delta^{15}\mathrm{N}_{Muscle} = 0.846 * \delta^{15}\mathrm{N}_{Bone} + 2.184$$

I then applied the muscle fractionation values from Hobson et al. (1996) in the mixing model to account for trophic enrichment between predator and prey (Mean ± SD: 1.3±0.1‰ for δ^{13}C; 2.4±0.3‰ for δ^{15}N).

3.3.2 Predator

Overall, Hector's dolphin bone collagen signatures ranged from -14.14‰ to -12.35‰ for δ^{13}C and from 13.91‰ to 17.00‰ for δ^{15}N (Table 3.1).

Table 3.1: Summary of the dolphin samples and their isotope signatures. All values represent bone collagen signatures except those for the nine muscle samples.

		δ^{13}C (‰)			δ^{15}N (‰)		
Dolphin Samples	*n*	**Mean ± SE**	**Min**	**Max**	**Mean± SE**	**Min**	**Max**
OVERALL							
Bone collagen	42	-13.1 ± 0.1	-14.1	-12.4	15.7 ± 0.1	13.9	17.0
Muscle	9	-16.1 ± 0.2	-17.0	-14.6	15.3 ± 0.2	14.3	16.2
SEX							
Male	19	-13.2 ± 0.1	-13.9	-12.3	15.5 ± 0.2	13.9	16.6
Female	21	-13.0 ± 0.1	-14.1	-12.4	16.0 ± 0.1	15.1	17.0
YEAR							
Before	28	-13.0 ± 0.1	-14.1	-12.3	15.9 ± 0.1	14.9	17.0
After	14	-13.3 ± 0.1	-13.9	-12.6	15.3 ± 0.2	13.9	16.4
AREA							
Inside	25	-13.0 ± 0.1	-14.1	-12.3	16.0 ± 0.1	14.3	17.0
Outside	17	-13.2 ± 0.1	-13.7	-12.6	15.3 ± 0.2	13.9	16.5

Differences in diet between sexes

On average, δ^{15}N was higher in females than males (mean difference: 0.55‰; 95% CI: 0.07 to 1.02‰; Figure 3.2). While the precision of this estimate is low, likely due to small sample size and individual variation in nitrogen signature, the positive confidence interval of the difference demonstrates significance. Female dolphins also had higher δ^{13}C signatures than males, but this difference was not statistically significant (mean difference: 0.26‰; 95% CI: -0.03 to 0.55‰).

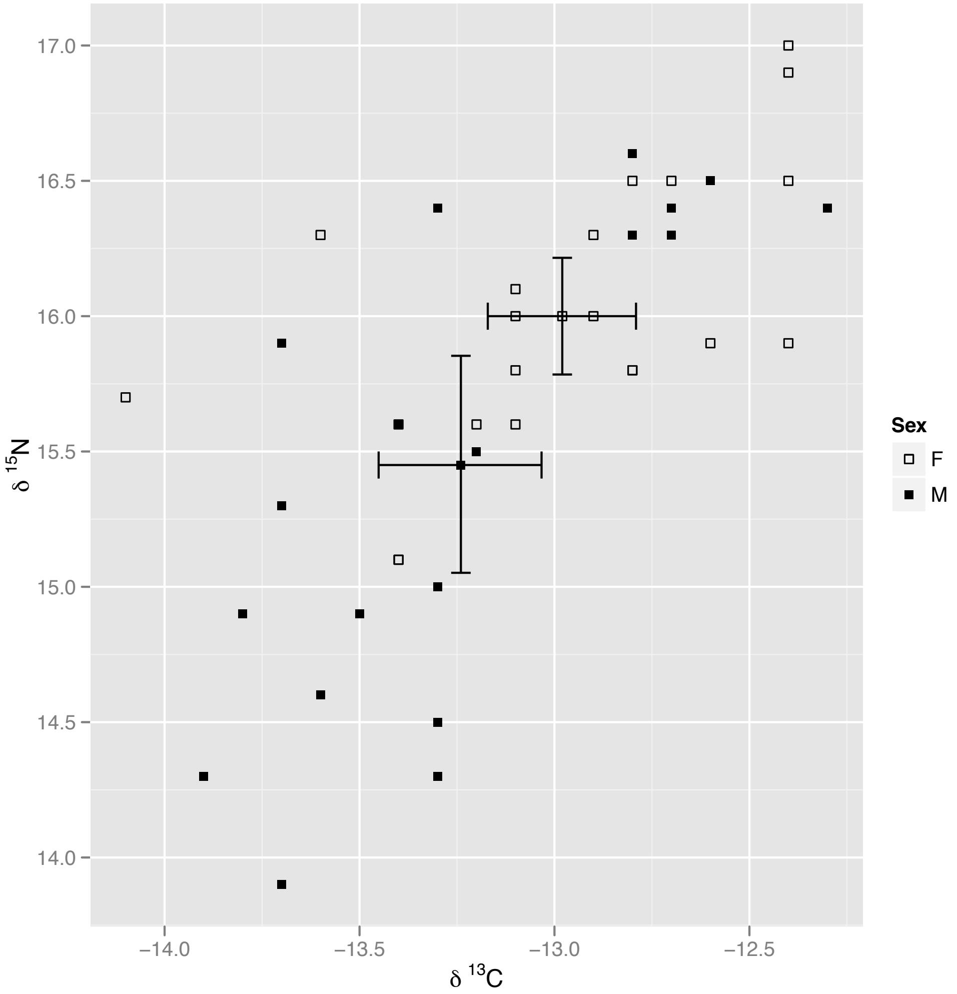

Figure 3.2: Isotope signatures of female & male dolphins with mean signatures & 95% CIs.

Effect of Banks Peninsula Sanctuary on diet

A two-way ANOVA found no significant interaction between 'Year' and 'Area' ($F_{2,36}$=0.940, P=0.400), implying that the introduction of the BPMMS has not had a significant effect on the isotope signature of the dolphins.

The data do, however, suggest that the dolphins' δ^{13}C signatures were significantly lower along the entire South Island east coast in recent years (post-2006) compared to pre-1988 (mean difference: -0.33‰; 95% CI: -0.62 to -0.03‰; Figure 3.3). Similarly, the nitrogen signature was significantly lower (mean difference: -0.61‰; 95% CI: -1.14 to -0.08‰; Figure 3.3).

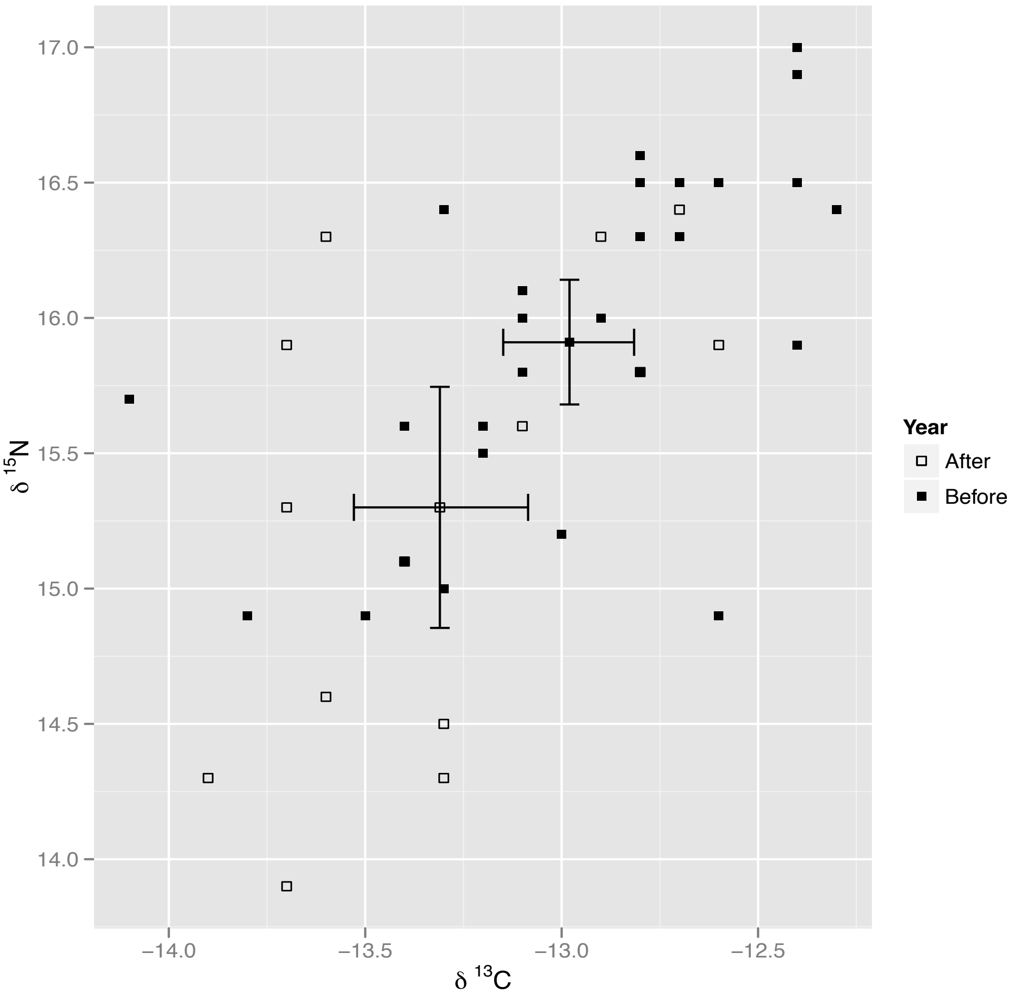

Figure 3.3: Isotope signatures of dolphins from before & after the Sanctuary creation with mean signatures & 95% CIs.

The nitrogen signatures were also significantly higher at Banks Peninsula compared to the rest of the South Island east coast, for all of the years examined (mean difference: 0.70‰; 95% CI: 0.25 to 1.15‰; Figure 3.4). There was no evidence of a difference in δ^{13}C between areas (mean difference: 0.15‰; 95% CI: -0.13 to 0.44‰; Figure 3.4).

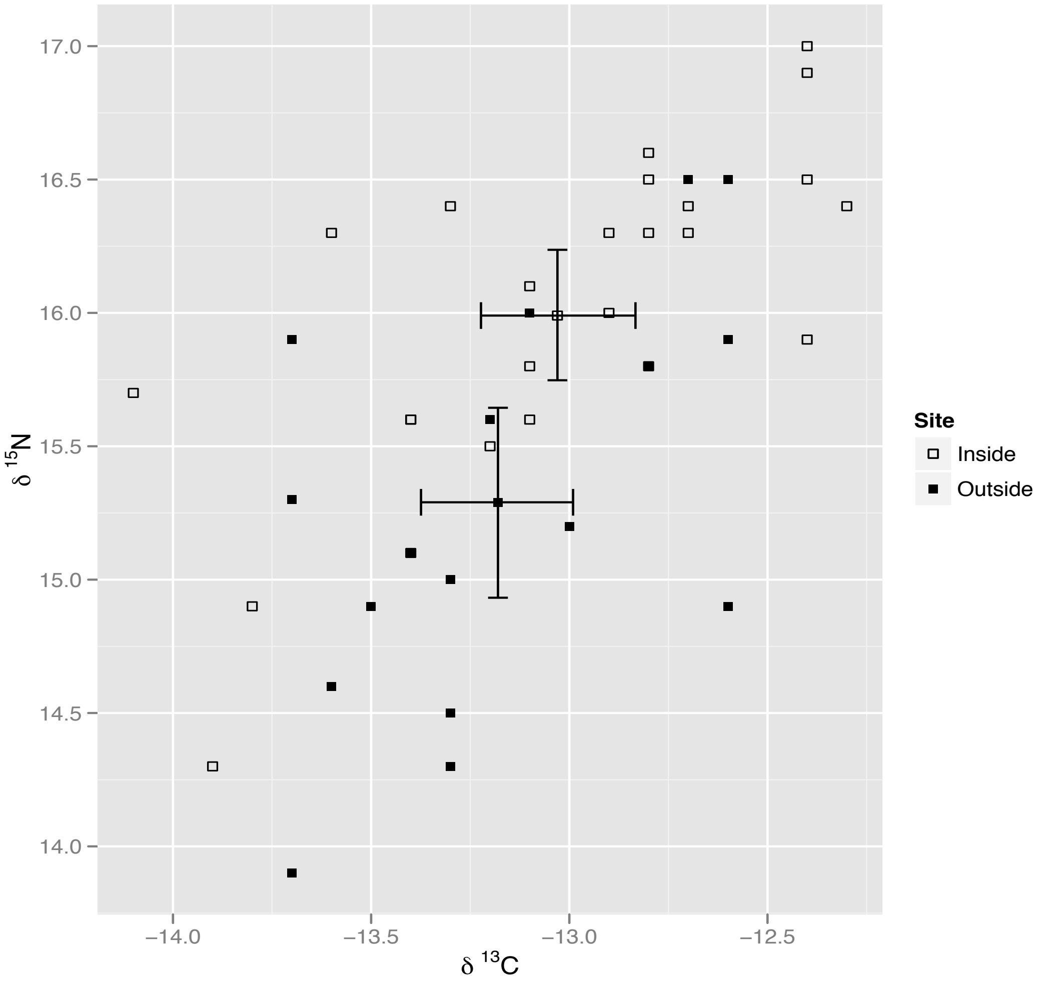

Figure 3.4: Isotope signatures of dolphins from inside & outside of the Sanctuary boundaries with mean signatures & 95% CIs.

3.3.3 Prey

Carbon signatures of prey ranged from -18.9 for blue warehou to -15.1 for sand flounder. Nitrogen signatures ranged from 9.9 for arrow squid to 16.7 for triplefin (Table 3.2).

Table 3.2: Summary of prey species sampled & their isotope signatures. Habitats are : EP=Epipelagic, BP=Benthopelagic, R=Reef associated, D=Demersal.

				δ^{13}C (‰)			δ^{15}N (‰)		
Prey		**Habitat**	***n***	**Mean ± SD**	**Min**	**Max**	**Mean± SD**	**Min**	**Max**
BONY FISH									
Sardinops neopilchardus	Pilchard	EP	5	-16.9 ± 0.4	-17.4	-16.4	12.8 ± 0.2	12.5	13.1
Pseudophycis bachus	Red cod	D	12	-16.9 ± 0.5	-17.8	-15.7	15.0 ± 0.8	14.0	16.4
Macruronus novaezelandiae	Hoki	BP	2	-16.9 ± 0.1	-17.0	-16.8	14.5 ± 0.4	14.2	14.7
Nemadactylus macropterus	Tarakihi	R	9	-17.5 ± 0.5	-18.4	-16.8	13.3 ± 0.8	12.2	14.7
Aldrichetta forsteri	Yelloweyed mullet	D	5	-17.6 ± 0.5	-18.2	-17.0	14.9 ± 0.5	14.2	15.6
Notolabrus celidotus	Spotty	R	6	-16.9 ± 0.3	-17.3	-16.6	14.7 ± 0.4	13.9	15.1
Geniagnus monopterygius	Spotted stargazer	D	3	-17.6 ± 0.4	-18.0	-17.3	14.0 ± 0.4	13.5	14.3
Forsterygion varium	Triplefin	R	6	-17.6 ± 0.3	-18.0	-17.2	15.7 ± 0.6	14.8	16.7
Parapercis colias	Blue cod	D	6	-16.9 ± 0.7	-18.0	-16.0	14.9 ± 0.7	14.0	15.8
Thyrsites atun	Barracouta	BP	1	-17.4			13.9		
Seriolella brama	Blue warehou	BP	6	-18.6 ± 0.4	-18.9	-17.8	14.0 ± 0.4	13.3	14.3
Pelotretis flavilatus	Lemon sole	D	5	-17.0 ± 0.2	-17.4	-16.8	13.4 ± 0.2	13.2	13.8
Rhombosolea plebeia	Sand flounder	D	5	-16.3 ± 0.8	-16.9	-15.1	14.3 ± 0.6	13.6	14.8
CARTILAGINOUS FISH									
Squalus acanthias	Dogfish	D	6	-17.2 ± 0.6	-18.0	-16.2	12.2 ± 1.0	11.0	13.3
Cephaloscyllium isabella	Carpet shark	D	1	-17.1			12.5		
CEPHALOPOD									
Nototodarus sloanii	Arrow squid	BP	3	-17.1 ± 0.2	-17.3	-16.9	10.9 ± 0.9	9.9	11.7
CRUSTACEAN									
Metacarcinus novaezelandiae	Piecrust crab	D	3	-16.2 ± 0.4	-16.6	-15.9	13.9 ± 0.3	13.7	14.2
Ovalipes catharus	Paddle crab	D	1	-16.2			13.1		
Nectocarcinus antarcticus	Red swimming crab	D	5	-16.2 ± 0.3	-16.5	-15.8	14.2 ± 0.4	13.6	14.6

Grouping by prey habitat

Mean δ^{13}C signature of benthopelagic prey was significantly lower than both demersal (mean difference: -0.97‰; 95% CI: -1.52 to -0.42‰) and epipelagic prey (mean difference: -0.96‰; 95% CI: -1.87 to -0.05‰) (Figure 3.5). Mean δ^{13}C of reef associated prey was 0.50‰ lower than demersal prey (95% CI: 0.06 to 0.94‰). Mean δ^{15}N signature was significantly higher in reef associated prey than both benthopelagic (mean difference: 1.10‰; 95% CI: 0.01 to 2.21‰) and epipelagic prey (mean difference: 1.59‰; 95% CI: 0.07 to 3.11‰). There was no evidence of a difference in mean δ^{13}C or δ^{15}N signature between the prey from other habitats. Discriminant analysis classified 58.89% of the samples successfully into their correct habitat group.

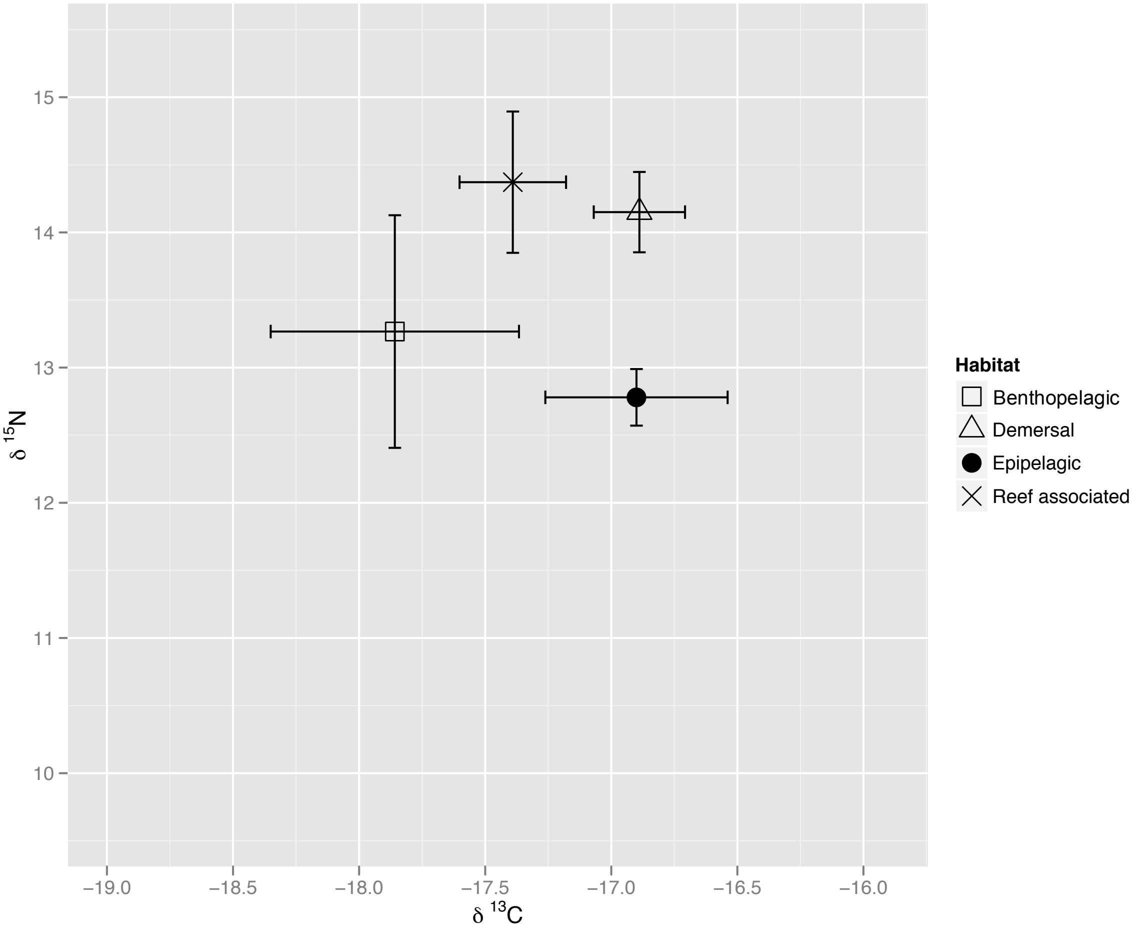

Figure 3.5: Mean isotope signatures of prey grouped by habitat with 95% CIs.

Grouping by prey taxonomic group

The mean δ^{13}C signature of crustaceans was significantly higher than that of both bony fish (mean difference: -1.04‰; 95% CI: -1.66 to -0.41‰) and cartilaginous fish (mean difference: -0.99‰; 95% CI: -1.88 to -0.10‰) (Figure 3.6). Mean δ^{15}N signature was significantly higher in crustaceans than both cephalopods (mean difference: 3.07‰; 95% CI: 1.41 to 4.72‰) and cartilaginous fish (mean difference: 1.71‰; 95% CI: 0.46 to 2.96‰), and higher in bony fish than both cephalopods (mean difference: 3.41‰; 95% CI: 1.95 to 4.88‰) and cartilaginous fish (mean difference: 2.06‰; 95% CI: 1.08 to 3.04‰). There was no evidence of a difference in mean δ^{13}C or δ^{15}N signature among other taxonomic groups.

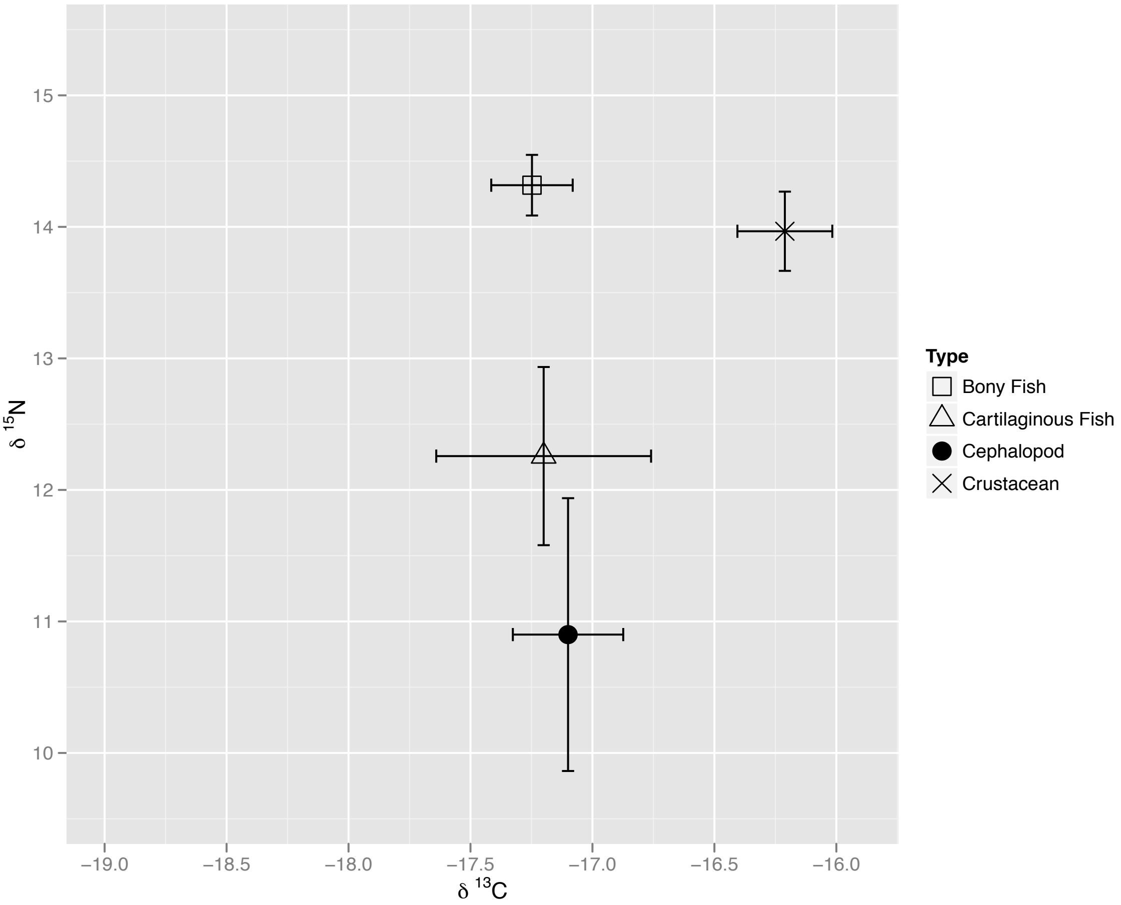

Figure 3.6: Mean isotope signatures of prey taxonomic groups with 95% CIs.

These differences were greater than those that I found among prey habitats and this is reflected in the more successful discriminant analysis results, where 82.22% of the samples were correctly classified by taxonomic group.

Cluster analysis

The 19 prey species were grouped using Ward's cluster analysis into six clusters. This number of clusters resulted in a high dissimilarity between clusters (Figure 3.7) and a low within-cluster spread (Figure 3.8). This spread, or variation in isotopic signature within clusters, increased steeply with fewer than six clusters (Figure 3.8). Separation into more than six, reduced the dissimilarity between clusters (Figure 3.7) while not greatly decreasing within-cluster spread (Figure 3.8).

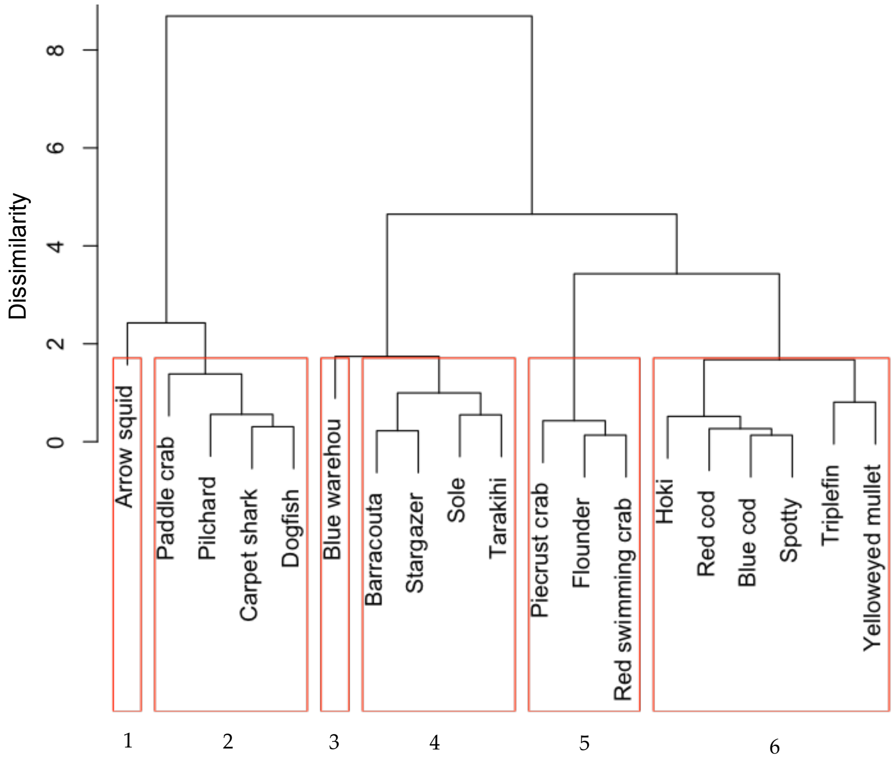

Figure 3.7: Cluster dendrogram highlighting the species composition of six clusters. Dissimilarity indicates the distance between clusters.

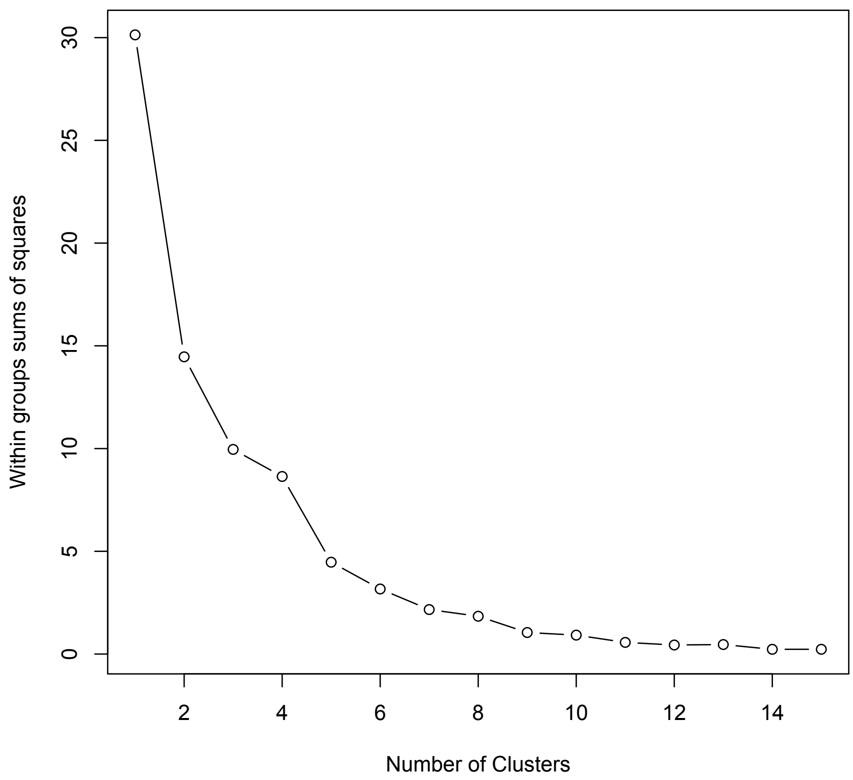

Figure 3.8: Scree plot of within-groups sums of squares indicating variation within clusters.

The clusters are mixed in terms of prey habitat (Figure 3.9A). Half contain only one habitat group, while the remaining half contain species from two or three different habitats. Both clusters 1 and 3 consist of only one species (Figure 3.7).

Taxonomic groups separate more clearly into clusters than prey habitats, with four out of the six clusters containing only one group of prey (Figure 3.9B). This clearer separation agrees with the results of the discriminant analyses. Clusters 3, 4 and 6 contain only bony fish and are where the majority of bony fish species are grouped. The cephalopod species falls by itself in Cluster 1. Cluster 2 is the most mixed in terms of taxonomic group, but contains both of the cartilaginous species.

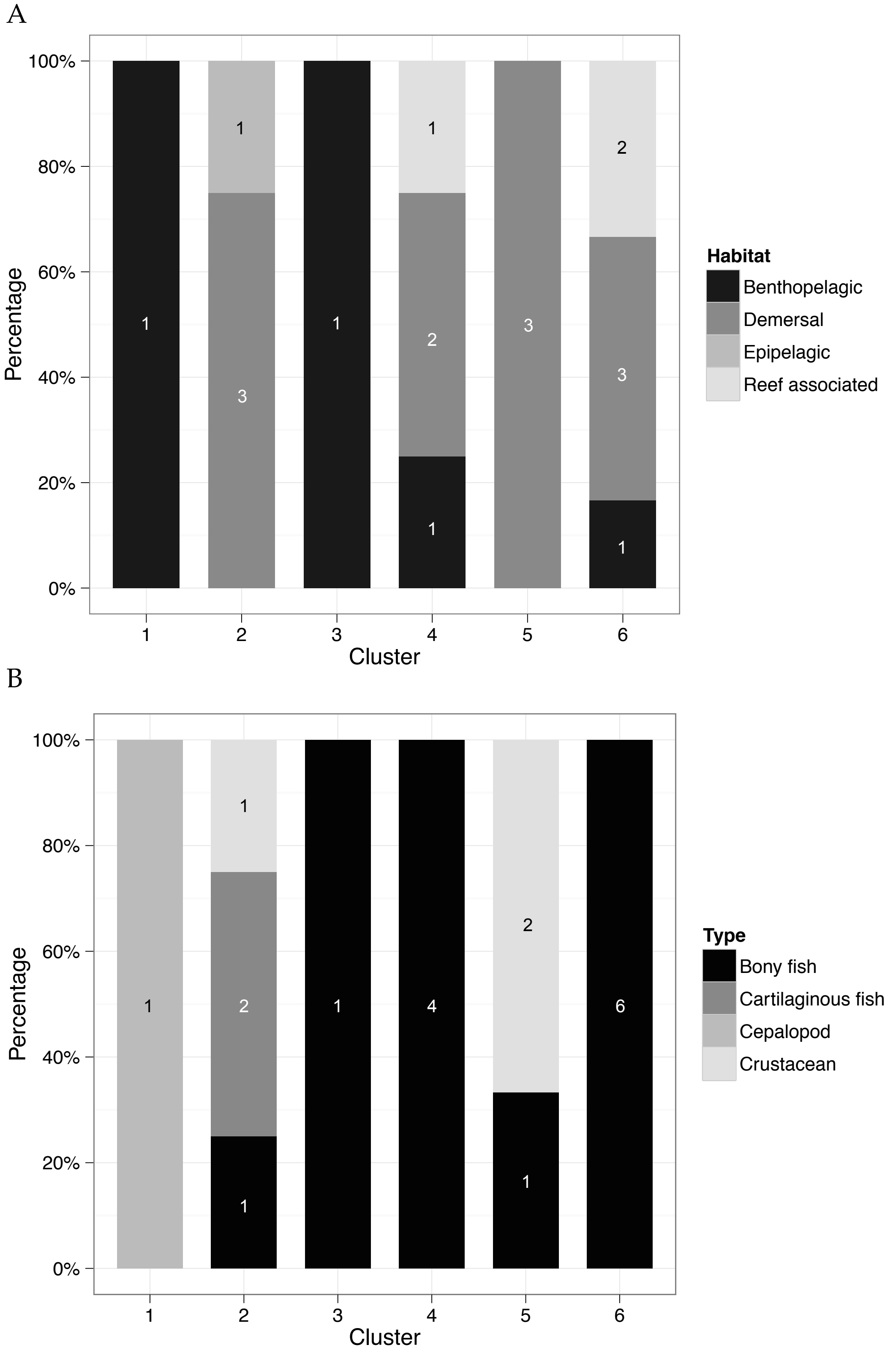

Figure 3.9: Cluster composition by prey habitat (A) and taxonomic group (B). Numbers within the bars indicate number of species in each group.

The difference in δ^{13}C signatures between clusters was most dominantly driven by the separation of clusters 3 and 5, and the difference in δ^{15}N signature driven mainly by the separation of clusters 1, 2 and 6 (Figure 3.10). Discriminant analysis was able to correctly classify 77.78% of the samples into their assigned cluster. This is more successful than when grouped by prey habitat, but not as successful as when grouped by taxonomic group.

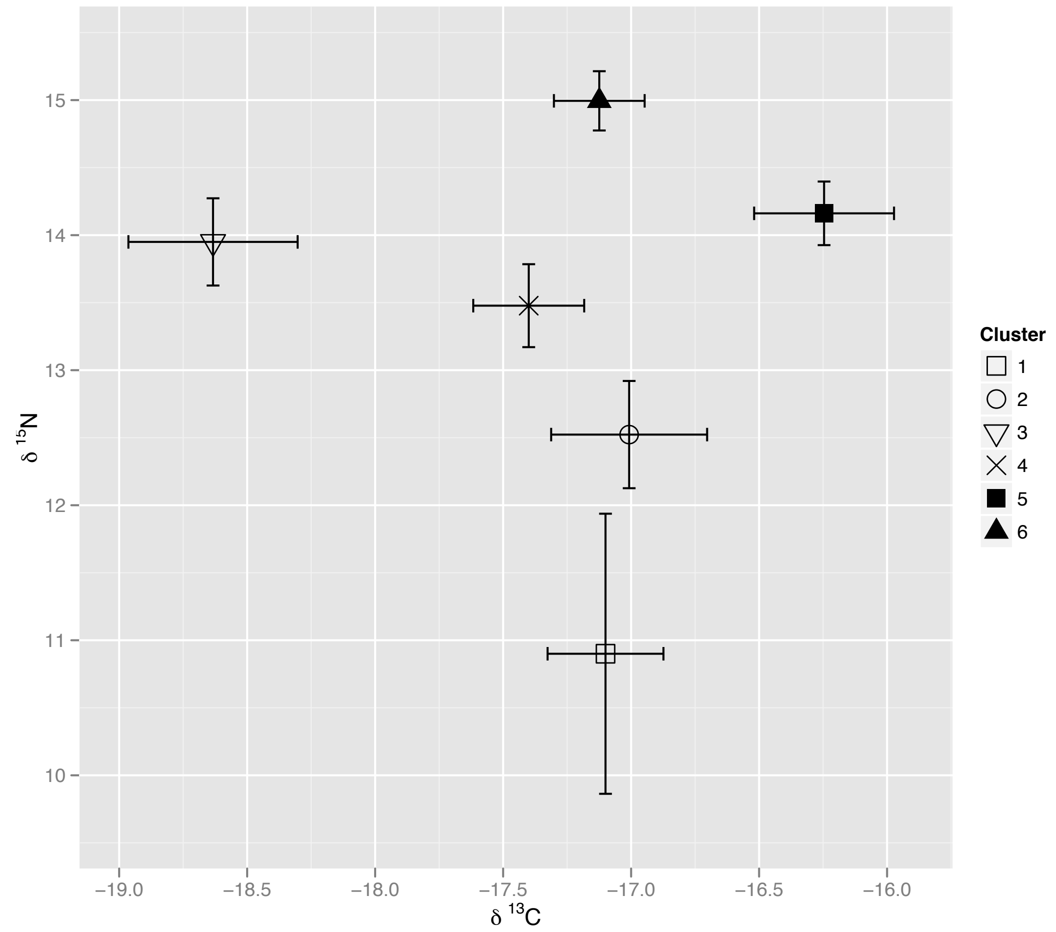

Figure 3.10: Mean isotope signatures of the six clusters with 95% CIs.

3.3.4 Diet analysis

As the discriminant analyses indicated that the prey isotope signatures were most successfully grouped by taxonomic group, I estimated the contributions of these four prey sources to the dolphins' diet.

Bony fish made the biggest dietary contribution (Figure 3.11). For female dolphins, this contribution was estimated between 33-60% of the diet (mode: 47%) while for males this estimate was slightly lower at 21-58% (mode: 40%). Cartilaginous fish also contributed to the dolphins' diet, though it is uncertain to what extent. They are most likely to make up 8-51% for females (mode: 34%), and 2-66% for males (mode: 38%). Cephalopods had a small contribution, particularly for females, and crustaceans contributed the least.

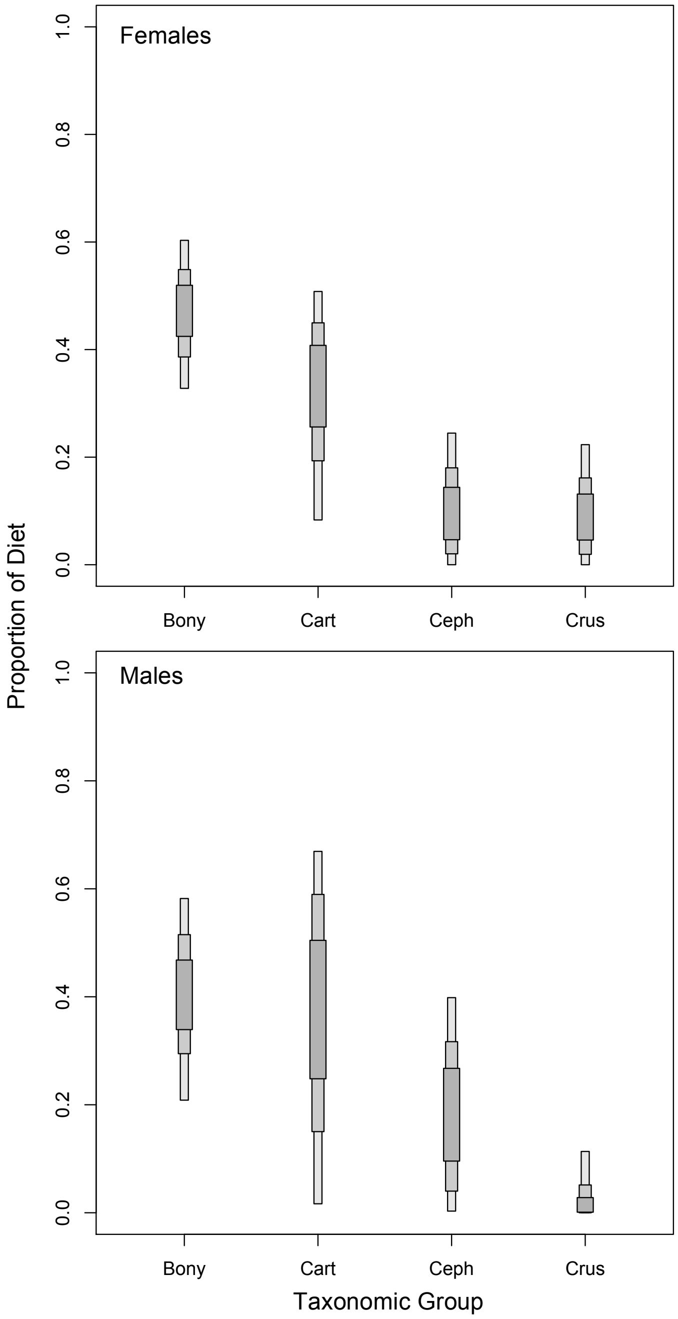

Figure 3.11: Range of possible contributions of different prey taxonomic groups to the diet of female & male dolphins. Decreasing bar widths represent 50%, 75% and 95% credibility intervals estimated from SIAR Bayesian mixing models.

As indicated in Section 3.3.3, there were also significant differences in $\delta^{13}C$ and $\delta^{15}N$ between prey from different habitats. As bony fish were the largest contributors, this prey group was examined in more detail, to determine whether species from particular habitats are more likely to be eaten (Figure 3.12). Epipelagic bony fish contributed the most for both females (mode: 57%, 95% CI: 45-68%) and males (mode: 51%, 95% CI: 28-69%; Fig. 3.11). Benthopelagic bony fish contributed more to the diet of males (mode: 35%, 95% CI: 20-48%) than females (mode: 24%, 95% CI: 8-37%).

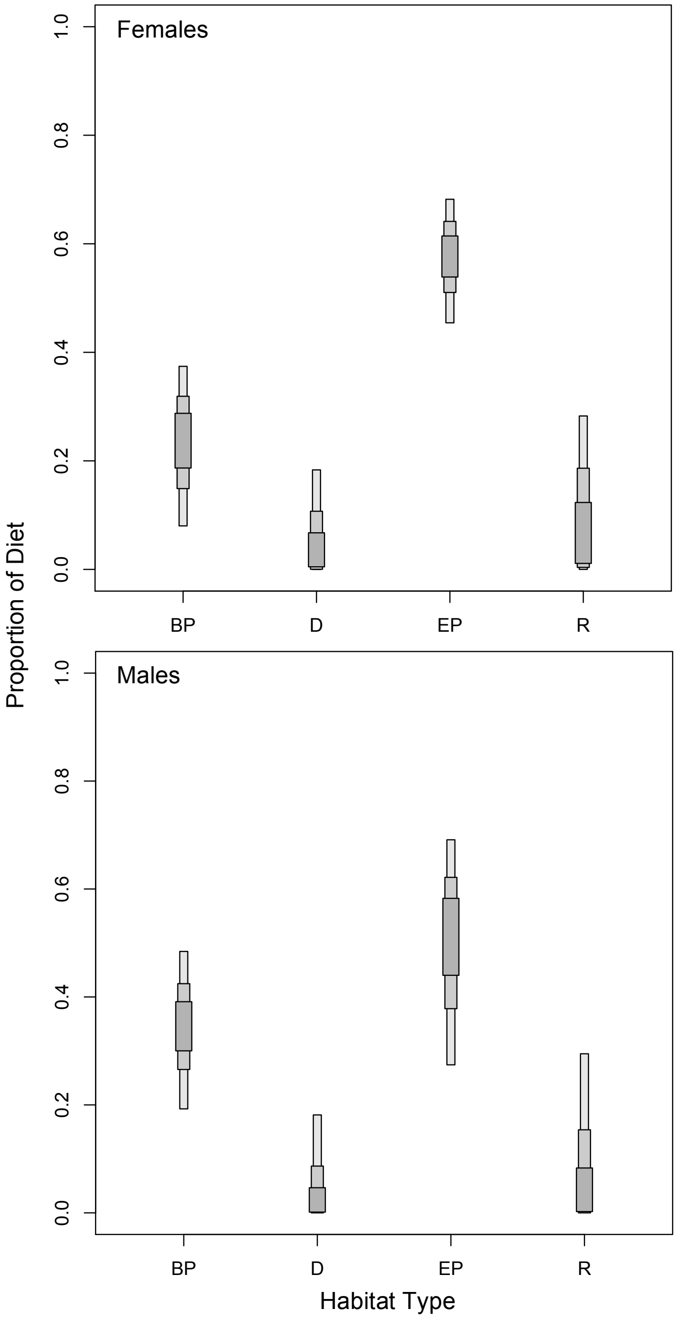

Figure 3.12: Range of possible contributions of different bony fish habitat types to the diet of female and male dolphins. (EP=Epipelagic, BP=Benthopelagic, D=Demersal, R=Reef associated). Decreasing bar widths represent 50%, 75% and 95% credibility intervals estimated from SIAR Bayesian mixing models.

The isotopic mixing space (Figure 3.13) highlights how the dolphins' signatures correspond to bony fish from these four habitat groups. This plot suggests that while contribution from benthopelagic, reef and demersal fish provide higher nitrogen values, a greater contribution from epipelagic prey appears to be resulting in the lower nitrogen signature of the dolphins. Similarly, the contribution of higher carbon values from three of the prey sources appears to be offset by the relatively large benthopelagic contribution, resulting in lower carbon signatures for the dolphins, particularly for males.

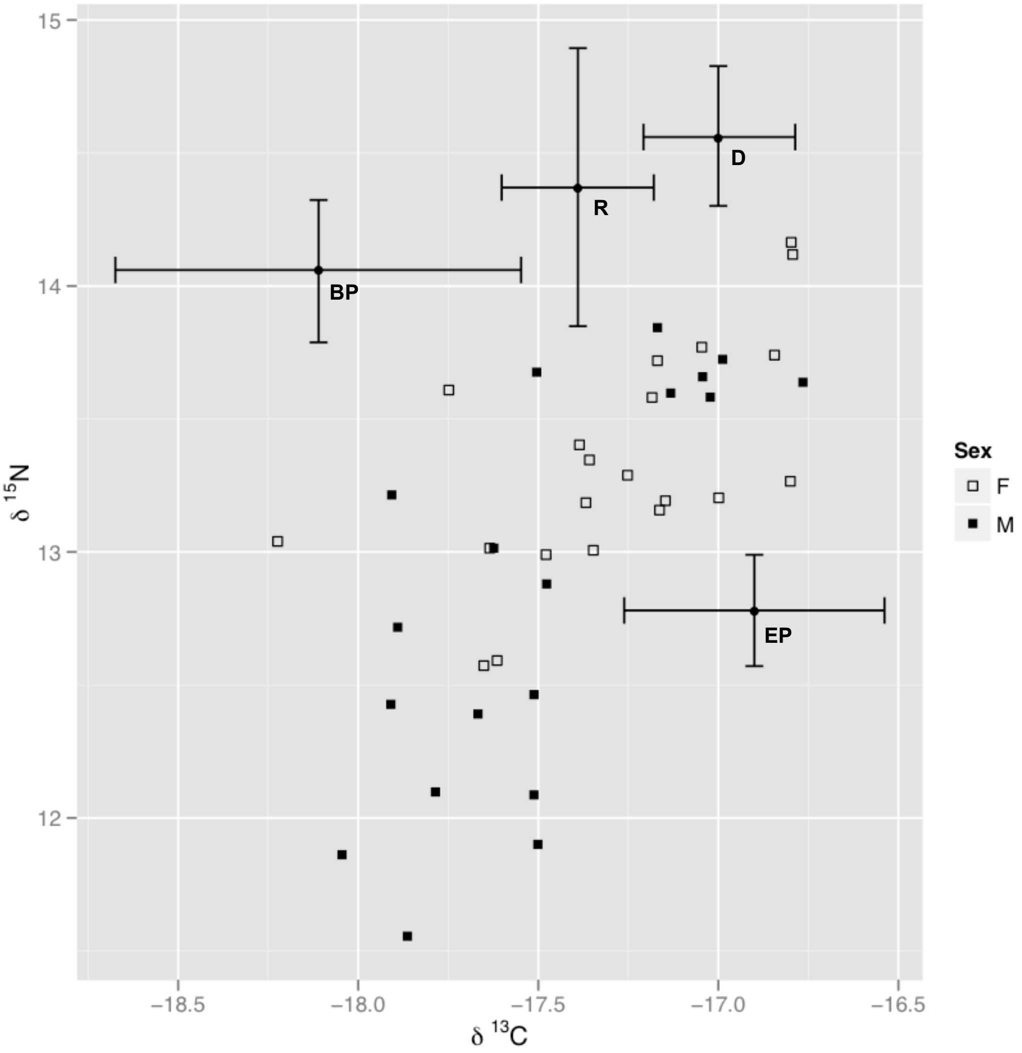

Figure 3.13: Isotope signature of female & male dolphins with mean signatures and 95% CIs of bony fish grouped by habitat type (EP=Epipelagic, BP=Benthopelagic, D=Demersal, R=Reef associated).

3.4 DISCUSSION

3.4.1 Diet analysis

These results indicate that male Hector's dolphins have significantly lower δ15N signatures than females. According to the diet analysis this could be due to greater consumption of cartilaginous fish and cephalopods by males, which have significantly lower nitrogen signatures than other taxonomic groups (Figure 3.6). Groups of Hector's dolphins at Banks Peninsula are often segregated by sex; for example all adults in nursery groups have been found to be female (Webster et al. 2009). Such sex segregation, particularly during the calving season, could lead to differences in foraging strategies between males & females. Lactating females in particular would be expected to have especially high nutritional demands.

I found no evidence that the creation of the Banks Peninsula Marine Mammal Sanctuary, and the associated change in fishing practice, has affected Hector's dolphin diet. It is important to remember however, that the analysis of bone collagen provides an indication of diet over the scale of years, and does not inform us of potential smaller scale, seasonal changes in diet that may have occurred over time. As only skeletal remains were available for the majority of individuals, it was not possible to assess dietary changes at a smaller scale using other tissues. If tissues such as muscle, blubber, and skin, are collected from future bycaught or beachcast animals, diet could be examined across a variety of timescales.

The dolphins did show significantly lower δ^{13}C & δ^{15}N signatures in recent years throughout the South Island east coast, and higher δ^{15}N signatures at Banks Peninsula than other areas. The average signatures of potential prey taxonomic groups (Figure 3.6) suggest that these patterns could be due to greater consumption of cartilaginous fish and cephalopods in recent years, and a greater contribution of demersal and reef fish to the diet of dolphins at Banks Peninsula. These trends in dolphin isotope signature may also originate from the base of the food web via changes in processes such as primary productivity or nutrient cycling (Peterson & Fry 1987). In coastal waters, influences from terrestrial inputs such as fertilizer and sewage can increase δ^{15}N of phytoplankton and subsequently the whole food web (Hansson et al. 1997, Peterson 1999). Climate-induced changes in prey resources can also result in changes to the diet of predators within or between trophic levels (e.g. Kaeriyama et al. 2004).

Overall, the diet analysis shows that individual dolphins prey on a variety of species of different groups, from throughout the water column. Bony fish were found to make the largest contribution to Hector's dolphin diet (Figure 3.11), followed by cartilaginous fish, which are likely eaten to some extent, perhaps more so by males. Within the bony fish, epipelagic species contributed the most (Figure 3.12) and as Figure 3.13 suggests, this appears to be due to all dolphins consuming prey from this habitat. Benthopelagic species appear to be consumed more by males than females, which again suggests potential differences in foraging strategy between sexes.

3.4.2 Limitations of this method

A potential limitation of the stable isotope modelling is the assumption that Hector's dolphin diet-tissue fractionation is similar to that observed in pinnipeds (Hobson et al. 1996), as mixing model results can be sensitive to variability in enrichment values (Bond and Diamond, 2011). It is not possible to derive enrichment estimates for Hector's dolphins directly, as this would require controlled feeding experiments of dolphins in captivity. The values for pinnipeds are therefore, the best estimate of fractionation available at this time, for this study and others like it (Newsome et al. 2010).

Another limitation of these data is that the prey were sampled between 2008 and 2011, whereas the dolphin samples date back to 1973. Prey samples available from earlier dates were preserved in alcohol, which can alter the stable isotope ratios of the tissue (Sweeting et al. 2004). Therefore, I was unable to assess any potential change in prey $\delta^{13}C$ & $\delta^{15}N$ over time and assume that prey signatures today are similar to those consumed by the dolphins across the course of this study. During the collection of prey, I was careful to ensure all samples came from Hector's dolphin habitat. Prey species were either captured during my own fieldwork, or collected by local fishermen trawling in Banks Peninsula coastal waters. The species analysed were limited by the samples able to be collected and analysis costs, however an effort was made to sample a representative selection of Hector's dolphin prey species from each of the prey sources identified in stomach content analysis (Miller et al. 2013).

Mixing models are sensitive to missing prey sources and will give biased estimates of dietary contributions if some are excluded (Phillips et al. 2014). In the future it would be valuable to analyse additional epipelagic prey in particular, as that group consisted of only pilchard. The discriminatory power of mixing models generally decreases however, as the number of sources increases, depending upon the isotopic separation of sources. For predators which feed on a large number of similar prey species, the overlap in prey isotope signatures inhibits models from estimating the contribution of prey to species level, as can more easily be done through stomach content analysis. Instead, stable isotope analysis may only allow coarse patterns of consumption to be inferred. Although this was the case with Hector's dolphins, prey were able to be successfully combined into distinct groupings that were ecologically meaningful. Ultimately, it is necessary to find a balance in which all isotopically distinct prey sources are represented while retaining discriminatory power (Phillips et al. 2014).

3.4.3 Comparison with stomach content analysis

The key differences between the stable isotope analysis and stomach content results of Chapter 2, highlight the benefits of combining both methods to gain a more comprehensive understanding of dietary preferences. While the stable isotope mixing model shows that epipelagic bony fish were the biggest dietary component, these prey were only of moderate importance in the stomach content results. Fish associated with the seafloor such as red cod and ahuru were found in a greater number of stomachs and contributed more in terms of mass and number eaten respectively. Another clear difference between the stable isotope and stomach content results is that the isotope data indicate a moderate contribution of cartilaginous fish to the dolphins' diet, particularly for males. In contrast, there were no remains evident in the stomach contents (e.g. dorsal spines), despite species such as dogfish being common within Hector's dolphin habitat (Beentjes et al. 2002). The stomach content results also showed no significant difference between the diet of males and females.

There are a few factors that are likely to contribute to the differences in findings between the two methods. The first important consideration is that the two methods examine diet over very different timescales. Stomach content analysis reveals prey recently ingested (Jobling & Breiby 1986, Pitcher 1980, Pierce & Boyle 1991), while stable isotope analysis of bone collagen represents assimilated diet over a timescale of years (Chisholm et al. 1982, Tieszen et al 1983, Dalerum et al. 2005). As a result, my stomach content results have a heavy seasonal bias, due to 84% of the samples being collected during spring and summer when Hector's dolphins are most frequently bycaught (Dawson 1991a). Although stable isotope analysis was only able to assess the contribution of prey species at a coarse taxonomic level, the broader timescale represented by this method was able to overcome the seasonal bias of stomach contents. It may be, that epipelagic bony fish contribute most on the timescale of years, while demersal species such as red cod have more seasonal importance, forming a large portion of the diet in the warmer months when these prey form higher densities inshore (Beentjes et al. 2002).

Hector's dolphins have been observed surface feeding on epipelagic prey (including pilchards and sprat) throughout the year, during this study and others (e.g. Bräger 1998). The limited information available on the distribution of these fish species in New Zealand suggests that they are present in near-shore surface waters year-round. For example, pilchards were caught during both winter and summer trawl surveys in the Hauraki Gulf between 1982-1997 (Paul et al. 2001). Sprat account for the majority of the diet of blue penguins (*Eudyptula minor*) throughout most of the year at Oamaru (Fraser and Lalas 2004), and during winter in Akaroa harbour, sprat were found to contribute most to the diet of juvenile chinook salmon (*Onchorhynchus tshawytscha*) (James and Unwin 1996).

Another important consideration is the potential bias in stomach content results caused by the different digestibility of prey species (Tollit et al. 1997). Sprat and pilchard otoliths, for example, are considerably smaller and more fragile than those of red cod. They may therefore, break down faster or become too eroded for identification, leading to an underestimation of the importance of epipelagic prey. Other prey remains such as squid beaks, can be over-represented in stomach content analyses compared to fish, as they take longer to digest (Sekiguchi and Best 1997). If this is the case here, then the cephalopod portion of the stomach contents will represent ingested diet over a longer timeframe than the other remains, and potentially does not contribute as much to the dolphins' diet as Chapter 2 suggests.

Cartilaginous fish have no otoliths and so can be under-represented by stomach content analysis. The lack of other remains from cartilaginous fish, such as spines and teeth, in stomach contents (Chapter 2) is curious, and suggests that this species is perhaps more commonly consumed in winter, a period from which few stomach contents are available. The importance of cartilaginous fish in Hector's dolphin diet could potentially be clarified by the use of fatty acid analysis (Iverson et al. 2004). This would require fresh blubber to be sampled however (Budge et al. 2006), so could not be carried out for the dolphins examined in this study.

Other studies using both prey remains and stable isotope analysis have similarly found that the use of both methods allows a more complete characterisation of dietary preferences. (e.g. Burns et al. 1998). Stable isotopes have been used to examine the diet of Pygoscelid penguins over a longer timescale than is possible with stomach contents (Polito et al. 2011). As with my study, Polito et al. found that while stomach contents provided finer taxonomic resolution, stable isotope analysis could examine broad taxonomic levels that were biologically meaningful. Teirney et al. (2008) found both methods detected similar prey contributions to the diet of Adélie penguins (*Pygoscelis adeliae*), and by using stable isotopes they were able to examine diet over periods of time when stomach contents are unable to be sampled. Both methods have also detected similar results for pinnipeds (Dehn et al. 2007), however the results of stable isotope analysis were at times inconclusive due to the numerous prey species. Davis et al. (2012) reported that for tropical fish with diverse feeding habitats, it was necessary to use stomach content results to understand the trophic complexity of stable isotope analyses. Overall, due to the limitations associated with both methods, their use in combination can be a more powerful tool for comprehensively studying consumer-resource relationships.

Conclusion

Stable isotope analysis of Hector's dolphin bone collagen has indicated that bony fish contribute the most to the dolphins' diet. By combining the results of this chapter with those from the stomach content analysis, we now have information on Hector's dolphin diet over both short and longer timescales. The use of stable isotopes was able to overcome some of the biases inherent with stomach content analysis and augment the results from Chapter 2 to gain a broader understanding of the relative importance of potential prey. While the stomach content results showed that demersal prey are the greatest contributors over spring and summer seasons, stable isotope models suggest that epipelagic bony fish have a greater long-term contribution. The results also indicate that there are both temporal and spatial differences in diet, as well as variation between sexes.

Using this information as a baseline, future sampling could further explore potential dietary patterns at different scales and examine what influence the availability of prey may have on dolphin distribution and population recovery. Hector's dolphins have a patchy distribution (Dawson et al. 2004, Rayment et al. 2011), with seasonal trends in offshore distribution (Rayment et al. 2010), and prey availability is often assumed a major driver of these distributional patterns (e.g. Bräger et al. 2003). Knowledge of the underlying factors directly associated with habitat use is particularly important in areas where spatial management measures are used. Such information may help predict situations in which the risk of fisheries competition is high, as well as areas where there is greater potential for recovery in an impacted and changing environment.

CHAPTER 4

HECTOR'S DOLPHIN HABITAT SELECTION AT BANKS PENINSULA

4.1 INTRODUCTION

Hector's dolphin (*Cephalorhynchus hectori*) distribution, like that of other animals, is influenced by the dynamics of their surrounding environment. Describing *how* animals are distributed is fundamental in ecology, and determining *why* they are distributed so is crucial for making predictions about how animals will respond to environmental change. The benefits of understanding the habitat preferences and ecological role of a species have been demonstrated in a variety of applications, from developing protected areas (Hooker and Gerber 2004, Cañadas et al. 2005), to predicting likely locations for population expansion (Thatcher et al. 2006, Guisan et al. 2013).

Habitat modelling is a valuable tool for identifying important environmental influences on cetacean habitat selection (Redfern et al. 2006). Associations between small cetaceans and a variety of factors have been described, including water depth (e.g. Cañadas et al. 2002, Ingram and Rogan 2002, Garaffo et al. 2010, Booth et al. 2013), sea-surface temperature (e.g. Gaskin 1968, Baumgartner et al. 2001, Forney et al. 2012), and salinity (e.g. Forney 2000, Torres et al. 2008, Forney et al. 2012). These factors however, may not influence cetacean habitat selection directly; it is often hypothesised that the distribution of cetaceans is driven mainly by the movements and abundance of their prey (e.g. Redfern et al. 2006, Torres et al. 2008, Dawson et al. 2013b).

In a review of cetacean habitat modelling techniques, Redfern et al. (2006) suggest that an ideal habitat model should incorporate prey data along with measurements of habitat variability. Only a few studies have correlated prey and dolphin distribution, and they have found varying results. While some evidence of strong overlap between dolphin and prey distributions has been found (Heithaus and Dill 2002, Benoit-Bird and Au 2003, Benoit-Bird et al. 2004, Heithaus and Dill 2006), other studies have concluded that the sampling resolution was insufficient to accurately define fine-scale overlap (Torres et al. 2008, MacLeod et al. 2013). The scale-dependency of predator-prey relationships varies with prey patchiness and predictability (Fauchald et al. 2000, Heithaus and Dill 2006, Redfern et al. 2006). If the aim of the study is to describe habitat selection over a relatively small area or short time frame, it is therefore important to gather data at a resolution that can capture variability in the system, at that scale. Furthermore, measurement of potentially important habitat parameters should be made concurrently.

Hector’s dolphin is a good candidate species for a study of fine-scale habitat selection, due to their coastal, well-documented distribution. Populations have been fragmented and reduced in size by gillnet bycatch since the 1970s (Slooten 2007), therefore nationwide, it is likely that the habitat use of the dolphins is more patchy than prior to the impact of this anthropogenic threat. Within populations however, the remaining dolphins show clear distributional patterns. They are year-round residents at Banks Peninsula, with small alongshore home ranges of approximately 50 km coastline length, and high site fidelity (Rayment et al. 2009b). Nationwide line-transect surveys have been conducted to assess their distribution and abundance (Dawson et al. 2004, Slooten et al. 2004), with an estimated 897 (CV = 28.2%; Dawson et al. 2004) individuals within the Banks Peninsula Marine Mammal Sanctuary. Hector’s dolphins have a patchy distribution at both nationwide and local scales (Dawson et al. 2004, Clement 2005), are generally distributed in shallow waters <90 m deep (Rayment et al. 2010), and regularly enter shallow bays and harbours (Dawson et al. 2013b). Within their depth range, their offshore distribution favours areas closer to shore in summer, but becomes more uniform in winter (Rayment et al. 2010). Alongshore, seasonal preferences for certain ‘hotspots’ have been found at Banks Peninsula, where dolphins are found in higher densities (Clement 2005). In Akaroa harbour, use of the inner harbour is much more frequent in summer than in winter (Dawson et al. 2013b).

Recent research has found correlations between the distributional patterns of Hectors' dolphins and oceanographic features, with dolphins showing preference for warmer waters (Bräger et al. 2003), and locations of frontal zones (Clement 2005). However, their seasonal patterns in movement are thought to be driven by movements of prey (Bräger et al. 2003, Clement 2005, Rayment et al. 2010, Dawson et al. 2013b), with several prey species showing inshore migration in warmer months (Paul 2000).

The goal of this work was to document patterns of Hector's dolphin habitat use around Banks Peninsula, and quantitatively assess relationships with both oceanography and prey availability. I describe seasonal distribution patterns throughout three regions: offshore, between alongshore sites, and within a large harbour. Data on the relative abundance of dolphins and prey are concurrently gathered, along with oceanographic measurements of the surrounding environment.

By using habitat models, I aim to investigate which factors drive the dolphins' seasonal movements within each region, and assess whether the inclusion of prey data improves model fit. The first subset of models contain only oceanographic variables, based upon the hypothesis that oceanographic data alone, provide a good prediction of Hector's dolphin relative abundance. Water temperature and water clarity are included as potential predictors, as these variables were found to correlate with the distribution of Hector's dolphin at Banks Peninsula by Bräger *et al*. (2003). Chilean dolphins have also shown preferences for warmer surface waters and areas of lower visibility (Heinrich, 2006). Other variables included are salinity, and chlorophyll *a*, which have been found to correlate with the distribution of bottlenose dolphins in parts of Florida Bay (Torres *et al.*, 2008).

The second subset of models, containing only prey predictor variables, are based upon the hypothesis that data on prey availability provide a better prediction of Hector's dolphin relative abundance. Variables explaining both general prey availability (species richness and diversity) are included, as well as data on a known important prey species (red cod mass). Prey availability has been found to be an important driver for other small cetacean species (e.g. Bottlenose dolphins: Heithaus & Dill, 2002; 2006; and Spinner dolphins: Benoit-Bird & Au, 2003).

In the third subset of models, oceanographic and prey predictor variables are combined, based upon the hypothesis that the inclusion of both data types provides a better prediction of Hector's dolphin relative abundance. Many previous studies examining small cetacean habitat selection in relation to abiotic variables have hypothesised that a key driver of patterns observed is prey availability, both in the case of Hector's dolphins (e.g. Bräger *et al.*, 2003; Clement, 2005; Rayment *et al.*, 2010; Dawson *et al.*, 2013) and other species (e.g. Karczmarksi *et al.*, 2000; Hastie *et al*, 2004; Heinrich, 2006).

4.2 METHODS

4.2.1 Data collection

Study site

This study was carried out at Banks Peninsula in the Canterbury region of the South Island east coast (Figure 4.1).

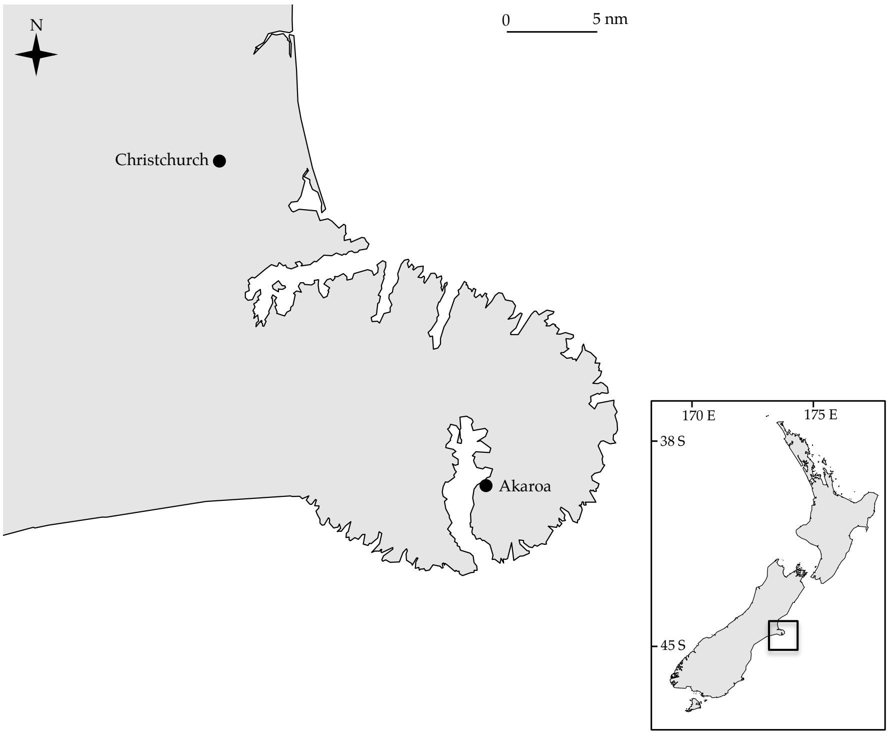

Figure 4.1: Location of the study area.

This area is a hotspot for Hector's dolphins on the east coast (Dawson et al. 2004, Clement 2005, Slooten 2007) and has been the site of ongoing research since 1984 (e.g. Slooten and Dawson 1988, Slooten et al. 1992, Bräger et al. 2002, Gormley et al. 2005, Rayment et al. 2010). The continental shelf around Banks Peninsula descends out approximately 90 km to the shelf break at 130-180 m deep (Herzer 1981). Akaroa Harbour is the largest bay around the Peninsula at approximately 16.5 km long, and is commonly used by Hector's dolphin throughout the year (Dawson 1991a, Dawson et al. 2013b).

New Zealand coastal waters are dominated by currents associated with the Subtropical Convergence; a boundary between warmer sub-tropical waters from the north, and cooler sub-Antarctic waters from the south. The Southland Current flows northward along the South Island east coast. The movement of water around Banks Peninsula is driven by the Southland Current, as well as the local effects of the tide, wind, and numerous river systems (Carter and Herzer 1979). The eastern boundary of the Southland current, known as the Southland front, changes between seasons, moving closer to the coastline during summer and autumn (Shaw 1998).

Overall study design

Surveys were carried out during every month of each season from autumn 2011 to summer 2012, and consisted of concurrent sampling of relative dolphin abundance, potential prey availability and oceanography from a 5.8 m aluminium power boat (R/V Grampus) with 2-3 people on board. Habitat use within three study regions was of interest: the offshore and alongshore habitat use around the Banks Peninsula coast, as well as the fine-scale distributional patterns within Akaroa Harbour.

The area surveyed on a particular day was determined by wind and swell conditions, with an effort to avoid sampling the same area on consecutive days. All surveys were carried out in sea states ≤ Beaufort 3, swell <2 m, and in good visibility. Data on relative dolphin abundance, prey availability and oceanography were collected concurrently in the chosen area, as detailed below.

OFFSHORE

To identify the drivers of offshore distribution patterns, I collected data in a stratified manner at three distances from shore: within 400 m (referred to as 0), and at 2 and 4 nautical miles (n.mi), on both the north and south sides of the peninsula (Figure 4.2).

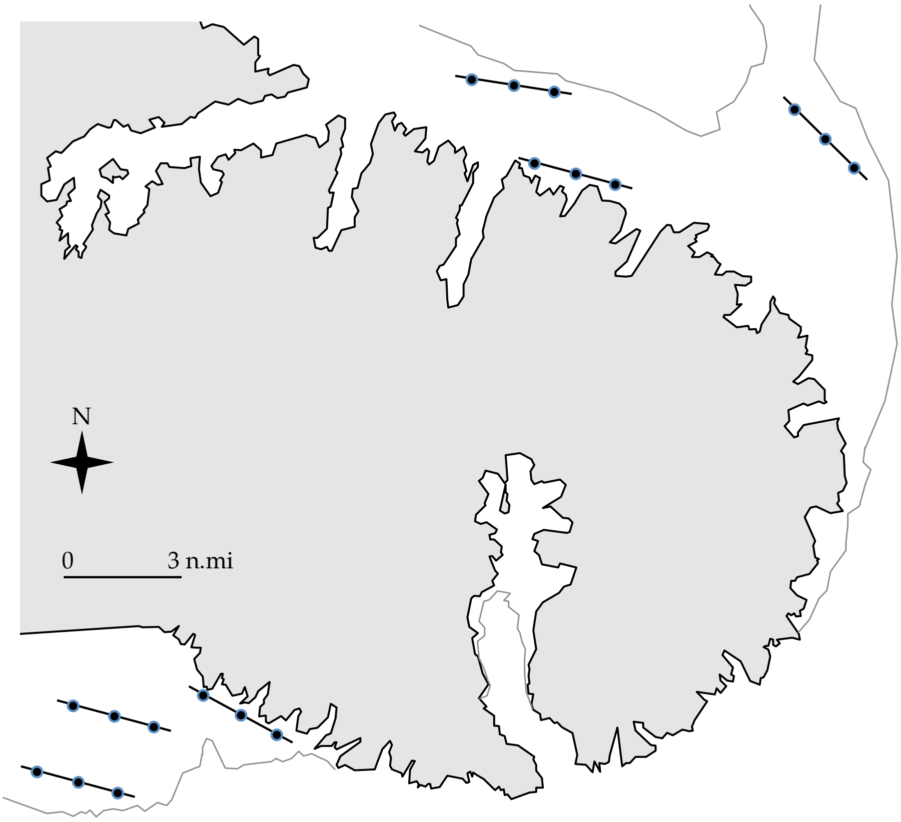

Figure 4.2: Map of the offshore sampling sites. Black lines represent 3 n.mi long transects surveyed on the north and south sides of Banks Peninsula at 0, 2, and 4 n.mi from shore. Black circles represent fish trap/oceanographic sampling locations. Grey contour shows the 20 m isobath.

Each offshore survey involved following a 3 n.mi long transect at one of the sampling distances on either the north or south side. To avoid confounding results with changes in water depth, transects were followed to maintain a consistent depth of 15-20 m. These two sides of the peninsula were surveyed to examine differences in offshore habitat preferences around the peninsula, and make the results more representative of the population as a whole. I did not survey the eastern side, as the deeper water in this area did not allow each distance from shore to be sampled.

ALONGSHORE

To identify drivers of alongshore patterns in dolphin distribution, I sampled three sites approximately 3 n.mi apart, along both the north and south sides of the peninsula (Figure 4.3).

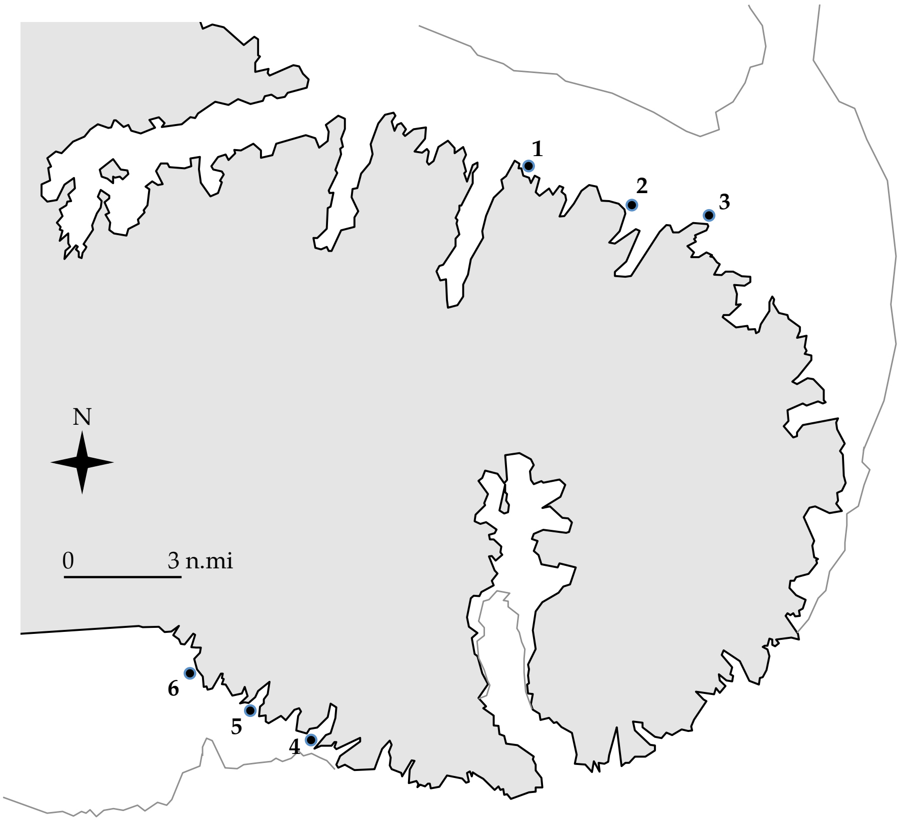

Figure 4.3: Map of the alongshore sampling sites along the (A) north and (B) south sides of Banks Peninsula (1: Wakaroa; 2: Decanter; 3: Long Lookout; 4: Peraki; 5: Te Oka; 6: Magnet). Black circles represent fish trap/oceanographic sampling locations. Grey contour shows the 20 m isobaths.

All areas were of comparable water depth (10-20 m). Each survey in this region involved collecting concurrent data on Hector's dolphins, prey, and oceanography on an alongshore transect. The transects ran approximately 500 m from shore, parallel to the coastline (as in previous photo-identification studies; e.g. Dawson and Slooten 1988) through the sites numbered in Figure 4.3. Any dolphins sighted within approximately 500 m of the survey sites were considered to be using that area.

HARBOUR

To identify drivers of the dolphins' distributional patterns within a large bay, I concurrently sampled three areas of Akaroa Harbour (the inner, mid, and outer harbour), corresponding to three depth ranges (5-10 m, 10-20 m, 20-25 m) (Figure 4.4).

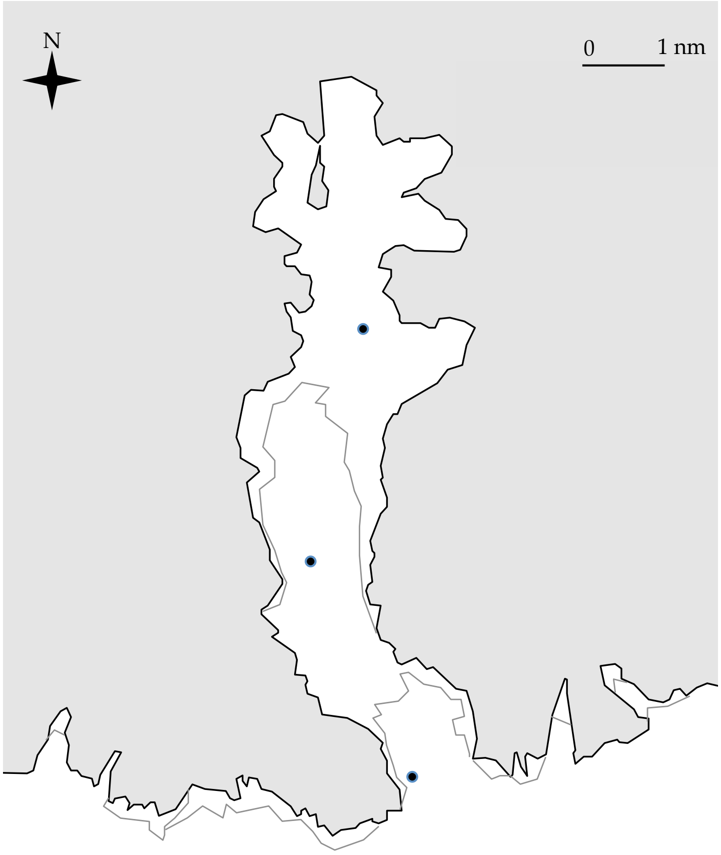

Figure 4.4: Map of the sampling locations within Akaroa Harbour. Black circles represent examples of fish trap/oceanographic sampling locations in the inner, mid, and outer harbour. Grey contours show the 10 and 20 m isobaths.

During each survey in this region, a standardised zig-zag transect (detailed in Dawson 1991a) was followed throughout the harbour, with the boat steered by GPS in reference to known landmarks. Each survey followed the same transect, with each leg measuring approximately 1 n.mi. in length. Any dolphins sighted within each of the three depth ranges were considered to be using that area.

Dolphin distribution

Data on the relative abundance of Hector's dolphins were collected by conducting ~1 km wide visual strip surveys along the transect chosen for that day (offshore, alongshore, or harbour). Two observers surveyed a strip of approximately 500 m on either side of the vessel, concentrating their effort to 90° on either side of the vessel trackline. Data were recorded on a palmtop computer (Hewlett Packard 200LX) with custom software and GPS interface. The time and GPS position were logged to a 'tracking' file every 60 seconds.

When a group of dolphins was sighted, the vessel was steered towards the group and was slowed to idle. I began the encounter on reaching the group, and logged the time and GPS position. Other data collected included information on the number of individuals, number of calves, behaviour state (primarily: long diving; traveling; active on surface; feeding; see Slooten 1994), and the presence & behaviour of any other species (e.g. white-fronted terns) interacting with or sighted close to the group. Depth (measured using a Humminbird Wide 2000 echosounder), Beaufort sea state, swell height, and sighting conditions were also recorded. If it was not possible to approach a group of dolphins closely (within ~15 m) in three attempts, or if a group was not re-sighted within ten minutes of first being seen, I estimated the number of individuals and their behaviour, and ended the encountered. This protocol aimed to minimise disturbance to dolphins that were avoiding the boat, and ensure consistency in search-effort. Photographs of any marked individuals were taken when possible, for use in future photo-identification studies. When more than one group was present at the same time, I recorded data for the new group separately. A group was defined as dolphins closely associating and engaged in similar activities, within approximately five body lengths of each other (Shane 1990). Once all data were recorded, I logged the time and GPS position again and ended the encounter before moving away.

To help assess dolphin presence or absence throughout the duration of the prey sampling, I attached T-PODs (Timing Porpoise Detectors; Chelonia Ltd, UK), autonomous acoustic data loggers, 1 m above each fish trap (see below). Using inbuilt filters set to match the click characteristics of Hector’s dolphins (Rayment et al. 2009a), these logged the presence of vocalising dolphins throughout the deployment of fishing gear, without the presence of the research vessel.

Potential Prey

I sampled potential prey availability using circular traps (Figure 4.5).

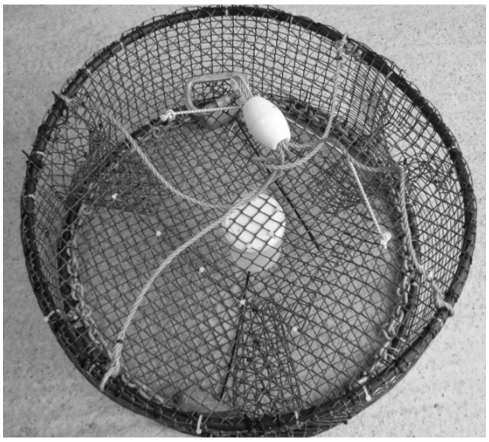

Figure 4.5: Fish trap design.

Each trap measured 70 cm in diameter and 30 cm in height. Bottom, top, and sides were made of ~ 1 cm wide plastic mesh. Three mesh funnels were located on the sides of the traps, leading towards the bait in the centre. Trap size was limited by the space on the research vessel. Similar fish surveys have found that catch rate does not generally increase with trap size however. Sheaves (1995) for example, found that larger traps caught more fish for only one of 22 species, and so recommended smaller traps for their practicality. Collapsible traps were trialled, but were deemed to be impractical for quick and easy use at sea.

Each trap had 6kg of weight around the base. A 2 kg danforth attached to the base with a short line was used to stop the traps being dragged by the tide. A lifeline clip at the top attached each trap to a nylon rope and surface buoy for easy retrieval. I baited each trap with ~200 g of thawed, chopped pilchard, chosen for its high oil content and proven effectiveness in similar fish surveys (e.g. Willis and Babcock 2000). The bait was contained in plastic jars with numerous small holes. Such a design has been found to give the highest catch rate and allow bait to last longer (Sheaves 1995).

The traps were set immediately prior to carrying out the dolphin survey and left to sample for a total of 3 hours (± 30 min). This usually allowed sufficient time to survey dolphins in the area and then retrieve the traps without being disturbed by changes in weather. Three hours was also deemed to be short enough to minimise escapement that has been associated with longer soak times (e.g. Whitelaw et al. 1991, Sheaves 1995). When surveying one of the offshore transects (Figure 4.2), a total of three traps were set along the 3 n.mi transect in the chosen area. Traps were set in the middle of each 1 n.mi transect segment. When surveying the alongshore sites (Figure 4.3), one trap was set at a randomised position in each bay, decided prior to surveying by placing a grid of numbers over a map of the area and choosing a number at random from a hat. During surveys of Akaroa Harbour (Figure 4.4), one trap was similarly placed randomly in each of the three survey areas.

The traps were designed to capture potential prey species <30 cm in length, living near the seabed, in particular red cod. This species was shown in Chapter 2 to contribute most to the mass of prey in the diet of Hector's dolphin. Species captured by the traps were identified, counted and measured (total length or carapace width). I released the majority of the catch alive, but retained selected individuals for use in the stable isotope analysis of Chapter 3. Animals collected were humanely euthanised (Ethics approval No. ET15/09). I logged time and GPS position at the start and end of each trap set and retrieval using the palmtop computer. Seafloor depth, Beaufort sea state, swell height, and visibility were also recorded, along with information on the number of dolphins and other species in the immediate area and their behaviour. All catch measurements were also recorded on the computer. If more than ten individuals of any species were present, as was often the case with crustaceans and occasionally fish, the first ten retrieved were measured and the total number caught were recorded. In this case, effort was made to retrieve individuals in a random manner, regardless of size or behaviour.

Oceanography

To collect data on water temperature, salinity, and chlorophyll (chl) *a* throughout the water column, CTD casts were conducted using a Seabird SBE-19 CTD profiler. This instrument included a Seabird SBE 5-01 submersible pump with temperature probe, conductivity grid, pressure port, and an additional WET Labs WETStar fluorometer. A CTD cast was carried out next to each fish trap immediately after it was set. The instrument was held at 1 m depth for at least 2 minutes to allow the sensors to equilibrate. It was then slowly lowered by hand to within approximately 2 m from the seafloor and back at a rate of approximately 0.5 m per second. Water clarity was measured at each set fish trap by lowering a 30 cm diameter secchi disk into the water and recording the depth at which it could no longer be seen. Secchi disk depths and the CTD cast number were recorded on the palmtop computer along with data on each fish trap.

4.2.2 Data exploration

Dolphin distribution

I determined dolphin presence or absence within each region by any encounters made while on-effort, setting/retrieving traps, and by any detections made on the T-PODs. T-POD data were accessed using the accompanying software, TPOD.exe, which applied a click train detection algorithm that classified logged clicks according to how likely they were to be of cetacean origin (Cet-Hi, Cet-Lo, Doubtful, Very Doubtful). I used only 'Cet-Hi' detections as confirmation of dolphin presence. As Hector's dolphins make high frequency, narrowband clicks that are easily distinguishable from other dolphins (Dawson and Thorpe 1990, Dawson 1991b), it is possible for the T-PODs to discriminate them from other sympatric cetaceans (Rayment et al. 2009a, Dawson et al. 2013b).

I extracted data on the number of individual dolphins encountered within each survey region, and included only those groups encountered while actively searching on-effort. For each offshore survey, the number of dolphins encountered was calculated as the average number of dolphins encountered on each of the three 1 n.mi transect segments (Figure 4.2). For each alongshore survey, I calculated the total number of dolphins encountered in the vicinity of each survey site (Figure 4.3). For each harbour survey, I calculated the total number of dolphins encountered within the inner, mid, and outer harbour (Figure 4.4).

Potential Prey

Prey species richness (total number of species) and diversity (Simpson's Diversity Index: $D=\sum(n/N)^2$), were calculated for each trap set. I estimated the mass of each red cod caught from its fork length, using the same power equations as in the stomach content analyses (Chapter 2, Appendix 1A). For the offshore surveys, where three traps were placed at 1 n.mi intervals along the transect, the average across the transect was used in analyses.

Oceanography

Using SBE Data Processing Software, I converted CTD data from digitised voltages into the physical quantities and their associated units, passed them through low-pass filters to remove spikes caused by debris, and aligned them in time relative to pressure. Data were then averaged into 1 m depth bins for analysis. The sea-surface and seafloor measurements for temperature, salinity, and chl *a* were then extracted for each cast. For the offshore surveys, where CTD and water clarity data were collected each 1 n.mi., the average across the transect was used in analyses.

To show how the measurements of each dolphin, prey and oceanographic variable differed among areas or seasons, I calculated 95% confidence intervals for the difference between means (Gardner and Altman 1986, Nakagawa and Cuthill 2007). If the confidence interval for a difference contained 0 in the case of oceanographic and prey variables, the data were consistent with no "significant" difference between the two means. In the case of dolphin encounter rate a multiplicative comparison was used, meaning that if the confidence interval contained 1 the data were consistent with no difference between the two means.

4.2.3 Habitat modelling

All analyses were carried out in R (R Core Team, 2013). I used generalised linear models (GLMs; McCullagh and Nelder 1989) and generalised additive models (GAMs; Hastie and Tibshirani 1990) to investigate which factors correlate with Hector's dolphin distributional patterns throughout the three regions of interest: offshore and alongshore at coastal Banks Peninsula, and throughout Akaroa harbour. Such models are commonly used to examine the relationship between the distribution of cetaceans and one or more habitat variables (Redfern et al. 2006). The number of dolphins encountered was used as the response variable. As this was found to follow a Poisson distribution, a log link function was used.

I examined sets of candidate models (Burnham and Anderson 2002), representing plausible alternatives based upon environmental correlations found in previous habitat studies of Hector's dolphins (Bräger et al. 2003, Clement 2005) and other small cetaceans (e.g. Torres et al. 2008, Forney et al. 2012), as outlined in the Section 4.1. The set of candidate models for each region included three subsets, comparing the influence of different potential drivers: oceanography, prey availability, and a combination of the two.

4.2.4 Model diagnostics and selection

Goodness-of-fit was examined for the most heavily parameterised model in the candidate set (Burnham and Anderson 2002). The dispersion parameter ϕ was calculated as the ratio of the residual deviance over residual degrees of freedom to test for overdispersion ($\varphi>1$; Zuur et al. 2009b). Multicollinearity among the predictor variables was assessed using Variance Inflation Factors (VIF; Brauner and Shacham 1998).

All candidate models were run as both GLMs and GAMs using the R package 'mgcv' (Wood 2006). The fit of each candidate model was assessed by AICc (Akaike Information Criterion; Burnham & Anderson, 2002), along with the percentage of deviance explained. AIC aims to select the model providing the best fit to the data, as measured by a decrease in variance and represented by a lower AIC score, while ensuring parsimony by minimising the number of predictor variables included. Models were ranked by ΔAIC from the best-fit model, with those models with a ΔAIC >7 having relatively poor support (Burnham et al. 2011).

A comparison of the residual deviance of the best-fit GLM and GAM was used to determine whether incorporating non-linear effects using additive modelling improves model fit, as is often the case with ecological data (Oksanen and Minchin 2002, Zuur et al. 2009b). In GLMs, the response variable (y) is modelled as a sum of linear relationships with a series of predictor variables ($x_1, x_2,\ldots, x_n$). GAMs extend this, by not constraining the relationship between x and y to be linear, and have been used successfully in previous studies on cetacean distribution to describe non-linear relationships with environmental variables (e.g. Forney 2000, Ferguson et al. 2005, Torres et al. 2008, Marubini et al. 2009).

4.3 RESULTS

4.3.1 Overall

Between autumn 2011 and summer 2012, I surveyed a total of 75 offshore, 68 alongshore, and 44 harbour transects (Table 4.1).

Table 4.1: Number of surveys carried out in each sampling region (Offshore, Alongshore, and within Akaroa Harbour) within each season and area.

OFFSHORE	***n***
Overall	75
SEASON	
Autumn	19
Winter	19
Spring	18
Summer	19
DISTANCE	
0 n.mi	25
2 n.mi	26
4 n.mi	24
SIDE	
North	37
South	38

ALONGSHORE	***n***
Overall	68
SEASON	
Autumn	15
Winter	17
Spring	18
Summer	18
SITE	
Wakaroa	12
Decanter	12
Long Lookout	8
Peraki	12
Te Oka	12
Magnet	12

HARBOUR	***n***
Overall	44
SEASON	
Autumn	9
Winter	9
Spring	15
Summer	11
AREA	
Inner	15
Mid	15
Outer	14

4.3.2 Dolphin distribution

OFFSHORE

Around the coast of Banks Peninsula, a total of 319 Hector's dolphins in 127 groups were encountered while on effort. Overall, dolphins were present at 58 of the 75 surveyed offshore transects.

At each of the three distances from shore, the number of dolphins encountered per nautical mile (n.mi) differed depending upon the season (Figure 4.6).

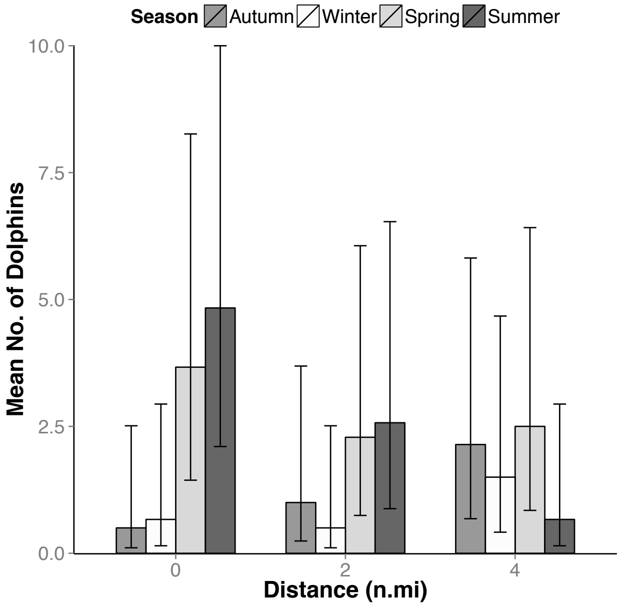

Figure 4.6: Mean no. of dolphins encountered per nautical mile around coastal Banks Peninsula for each season & distance from shore with 95% CI.

At both 0 n.mi and 2 n.mi from shore, the average number of dolphins in summer and spring was higher than in autumn and winter. The largest difference was found closest to shore (0 n.mi), where 9.67 (95% CI: 3.44 to 40.37) times more dolphins were encountered in summer than autumn, and 7.25 (95% CI: 2.85 to 24.45) times more in summer than winter. At 4 n.mi from shore during summer, the number encountered was 0.31 (95% CI: 0.009 to 0.86) times lower than in autumn.

Within some seasons, the average number of dolphins encountered differed depending upon the distance from shore (Figure 4.6). This was particularly the case during summer, when relative dolphin abundance at 0 n.mi was 1.88 (95% CI: 1.05 to 3.45) times higher than at 2 n.mi, and 7.25 (95% CI: 2.85 to 24.45) times higher than at 4 n.mi. Overall, there were 1.32 (95% CI: 0.95 to 1.84) times more dolphins encountered on the north side of the peninsula than the south, but this difference was not statistically significant.

ALONGSHORE

Alongshore, differences in dolphin numbers were found between the six survey sites (Figure 4.7).

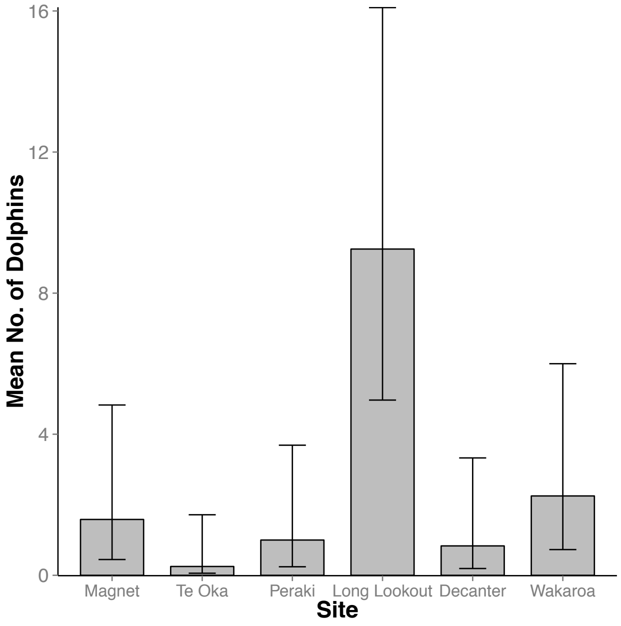

Figure 4.7: Mean no. of dolphins encountered within 500 m of each survey site with 95% CI .

There were more dolphins throughout the year at Long Lookout Point than all the other sites surveyed on both the north and south sides; from 3 (95% CI: 1.95 to 4.76) times more than at Wakaroa Bay, to 27 (95% CI; 10.6 to 110.36) times more than at Te Oka Bay. Te Oka Bay had fewer dolphins throughout the year than all the other alongshore sites.

HARBOUR

Within Akaroa Harbour, a total of 48 Hector's dolphins in 25 groups were encountered while on effort. Overall, dolphins were present during 22 of the 44 surveyed harbour transects. The number of dolphins encountered differed depending upon the area of the harbour and the season (Figure 4.8).

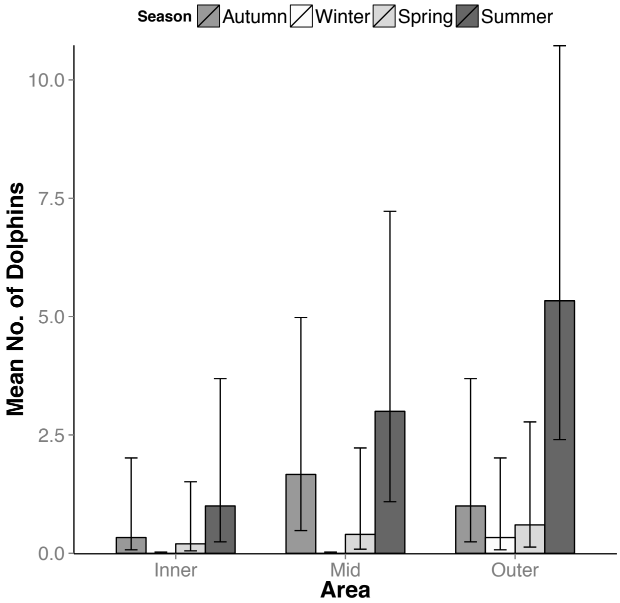

Figure 4.8: Mean no. of dolphins encountered each season within the inner, mid, and outer areas of Akaroa Harbour (Figure 4.4) with 95% CI.

Throughout the year, there were 3.17 (95% CI: 1.34 to 8.70) times more dolphins in the middle harbour than the inner harbour, and 4.64 (95% CI: 2.01 to 12.58) times more in the outer harbour compared to the inner. Throughout all areas, the number of dolphins encountered was greatest in summer.

4.3.3 Potential prey

Overall, 2583 animals comprising 15 species were caught in traps set around coastal Banks Peninsula (*n*=225) and Akaroa Harbour (*n*=44). Total catch included five species of teleost fish, two elasmobranchs, one agnathan, six crustaceans, and one mollusc species (Table 4.2).

The size of individuals ranged from a 1.2 cm wide red swimming crab to a 67.2 cm long dogfish. Red cod were caught on 63 out of 119 surveyed transects and were the most frequently caught prey species of known importance to Hector's dolphin diet (Miller et al. 2013).

Table 4.2: A list of all species caught in traps set around Banks Peninsula, the number of individuals and the mean size ± SD. Size of fish measured as total length; size of crustaceans measured as carapace width.

Species captured		***n***	**Size (cm)**		
			Mean ± SD	**Min**	**Max**
TELEOSTS					
Pseudophycis bachus	Red cod	174	19.2 ± 2.5	12.3	25.3
Nemadactylus macropterus	Tarakihi	8	13.2 ± 2.8	10.1	17.1
Notolabrus celidotus	Spotty	11	14.4 ± 3.5	9.2	20.9
Forsterygion sp.	Triplefin	65	7.1 ± 1.0	4.5	9.3
Hippocampus abdominals	Seahorse	1	22.5	22.5	22.5
ELASMOBRANCHS					
Cephaloscyllium isabellum	Carpet Shark	1	33.1	33.1	33.1
Squalus acanthias	Dogfish	119	31.9 ± 10.7	13.4	67.2
AGNATHANS					
Eptatretis cirrhatus	Hagfish	3	66.7 ± 30.6	40	100
CRUSTACEANS					
Pagurus novizealandiae	Hermit crab	980	3.9	1.4	5.8
Metacarcinus novaezelandiae	Piecrust crab	284	8.6 ± 1.9	3.1	15.5
Ovalipes catharus	Paddle crab	170	4.2 ± 1.3	1.9	9.5
Nectocarcinus antarcticus	Red swimming crab	416	2.8 ± 0.6	1.2	4.4
Pontophilus australis	Sand shrimp	1	2.5	2.5	2.5
Notomithrax sp.	Decorator crab	1	4.4	4.4	4.4
MOLLUSCS					
Cominella sp.	Whelk	349	3.5	1.9	4.2

Species richness

OFFSHORE

Species richness around coastal Banks Peninsula was broadly similar year-round (Figure 4.9). The biggest change was observed between autumn and summer (mean difference: 0.39; 95% CI: -0.32 to 1.10). Species richness was, however, lower in traps set at 2 n.mi than 0 n.mi from shore (mean difference: -0.88; 95% CI: -1.50 to -0.26), and a slightly greater number of species caught on the south side than the north (mean difference: 0.69; 95% CI: 0.19 to 1.19).

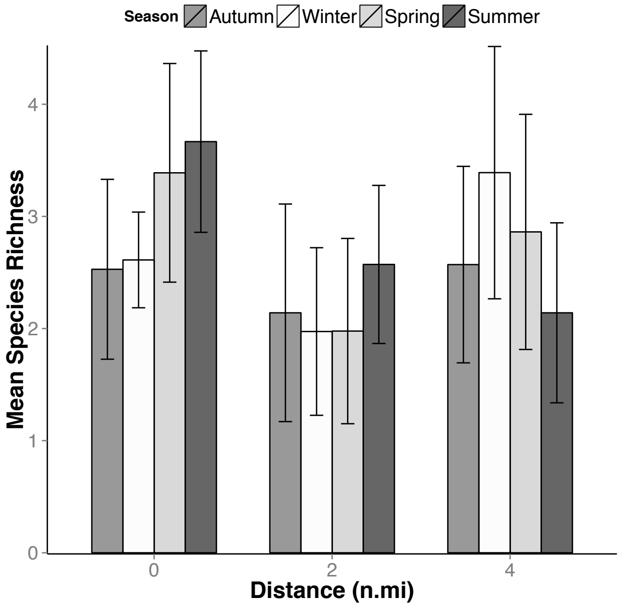

Figure 4.9: Mean species richness per trap set around coastal Banks Peninsula for each season and distance from shore with 95% CI.

ALONGSHORE

Differences in species richness were found between alongshore sites. Most notably, there was lower species richness at Decanter and Wakaroa Bays than all the southern sites surveyed (Figure 4.10).

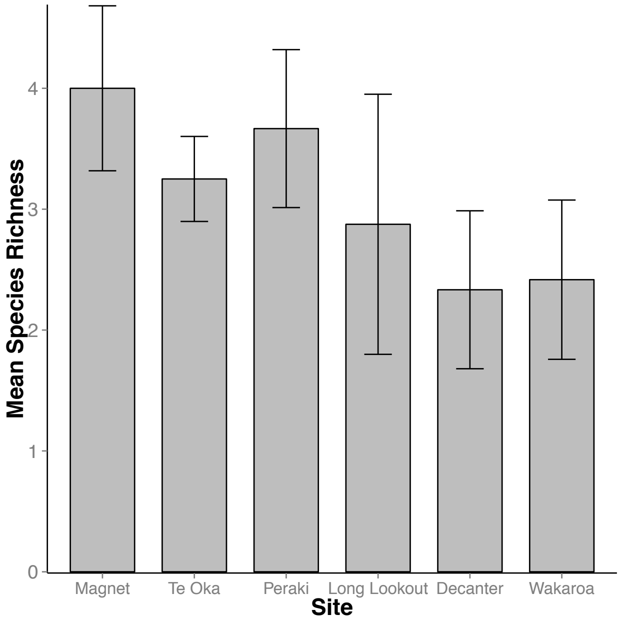

Figure 4.10: Mean species richness per trap set at each alongshore site with 95% CI.

HARBOUR

Within the mid and outer areas of Akaroa Harbour, species richness differed depending upon the season (Figure 4.11). This was particularly the case in the mid harbour, where more species were captured in autumn and summer than winter (mean difference autumn: 2.33; 95% CI: 1.17 to 3.50; mean difference summer: 2.92; 95% CI: 1.83 to 4.01), or spring (mean difference autumn: 2.47; 95% CI: 1.42 to 3.51; mean difference summer: 3.05; 95% CI: 2.09 to 4.01).

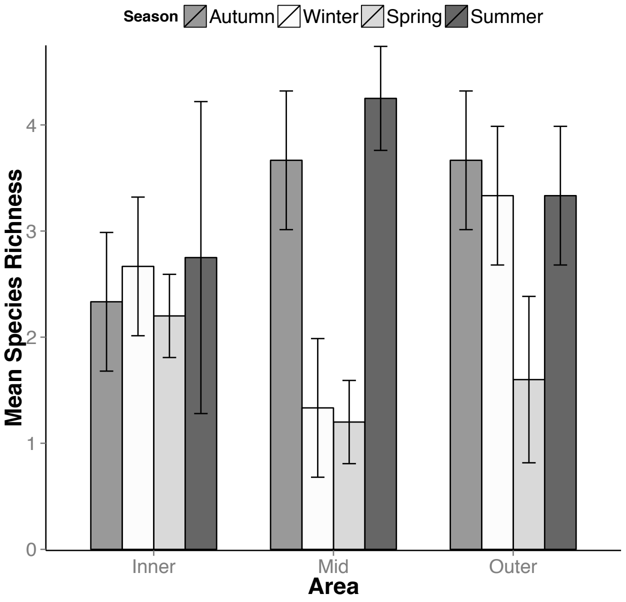

Figure 4.11: Mean species richness per trap set each season within the inner, mid, and outer areas of Akaroa Harbour with 95% CI.

Species diversity

OFFSHORE

Around the coast, the mean species diversity in traps (Figure 4.12) was similar among seasons, distances from shore, and sides of the peninsula.

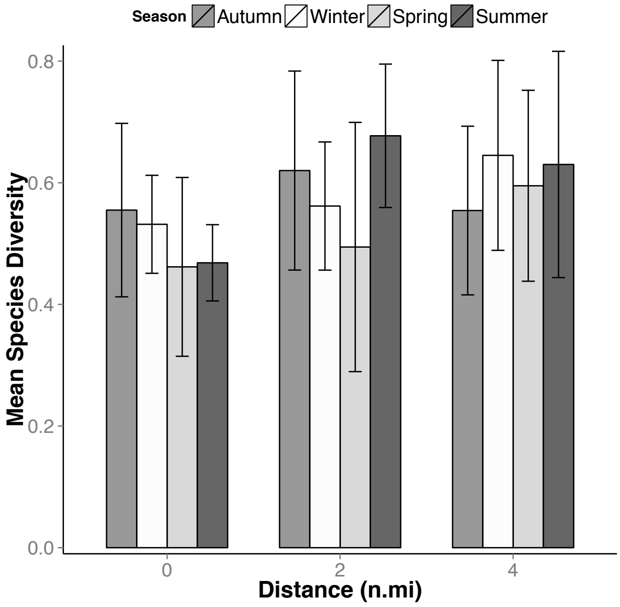

Figure 4.12: Mean species diversity per trap set around coastal Banks Peninsula for each season and distance from shore with 95% CI.

ALONGSHORE

There were no statistically significant differences in diversity between the surveyed sites (Figure 4.13), however there was a trend of slightly higher diversity in sites on the north side of the peninsula (Long Lookout Point, Decanter Bay, and Wakaroa).

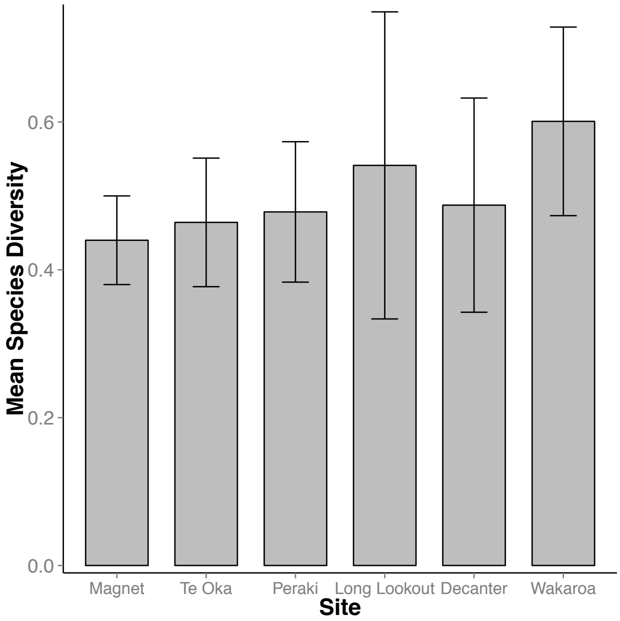

Figure 4.13: Mean species diversity per trap set at each alongshore site with 95% CI.

HARBOUR

Within the mid and outer areas of Akaroa Harbour however, species diversity differed depending upon the season (Figure 4.14). In the middle harbour in particular, there was a greater diversity of species was captured in winter and spring than in autumn (mean difference winter: 0.55; 95% CI: 0.26 to 0.84; mean difference spring: 0.57; 95% CI: 0.31 to 0.83), or summer (mean difference winter: 0.64; 95% CI: 0.37 to 0.92; mean difference spring: 0.66; 95% CI: 0.43 to 0.90).

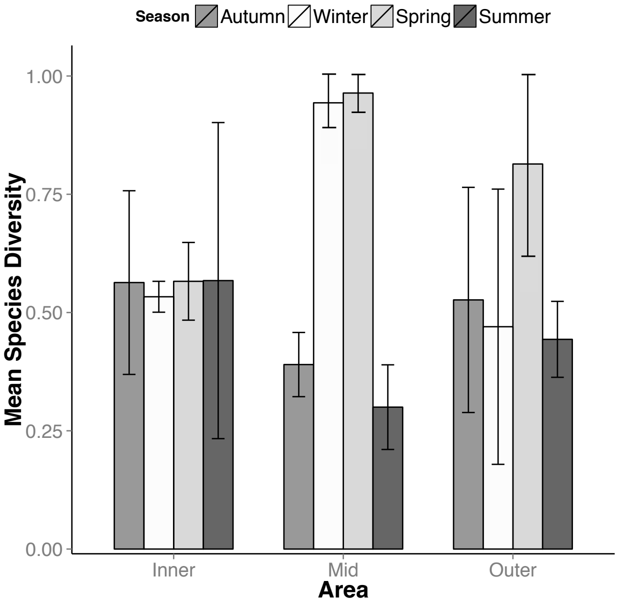

Figure 4.14: Mean species diversity per trap set each season within the inner, mid, and outer areas of Akaroa Harbour with 95% CI.

Red cod

Red cod was the species most frequently caught (53% of surveys) that is known to be an important component of Hector's dolphin diet (Chapter 2).

OFFSHORE

As with relative dolphin abundance, the average total mass of red cod caught per trap differed at each distance from shore depending upon the season (Figure 4.15). At 0 n.mi and 2 n.mi from shore, a greater mass of red cod was caught in summer and spring than in autumn and winter. The largest difference occurred at 0 n.mi, where on average, 125 g (95% CI: 80.22 to 170.73) more red cod was caught in summer than autumn, and none were caught in winter. At 4 n.mi from shore, the majority of red cod were caught in autumn and winter, while none were caught during summer.

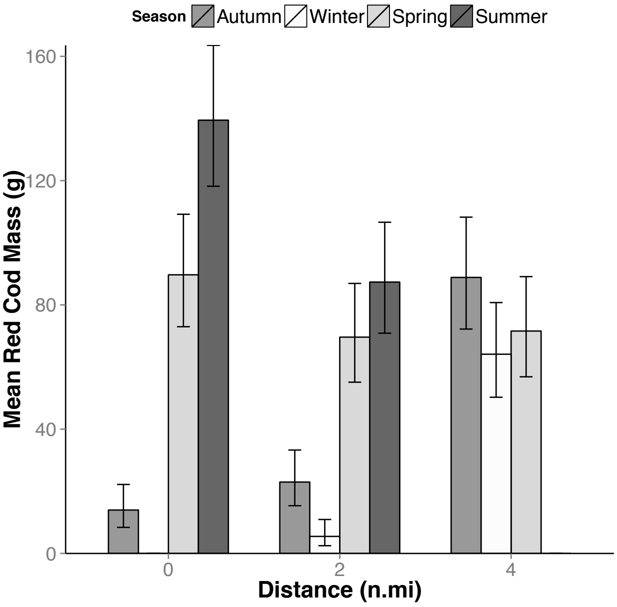

Figure 4.15: Mean mass of red cod caught per nautical mile around coastal Banks Peninsula for each season and distance from shore with 95% CI.

Overall, the amount of red cod caught in summer was greater at 0 n.mi than both 2 n.mi (mean difference: 52.10 g; 95% CI: 8.49 to 95.71), and 4 n.mi (mean difference: 139.45 g; 95% CI: 94.19 to 184.70). During both autumn and winter however, catch was greater at 4 n.mi than both 0 n.mi (mean difference autumn: 74.86 g; 95% CI: 31.25 to 118.47; mean difference winter: 64.12 g; 95% CI: 18.87 to 109.38) and 2 n.mi (mean difference autumn: 65.86 g; 95% CI: 22.25 to 109.46; mean difference winter: 58.65 g; 95% CI: 13.39 to 103.90). A slightly greater amount of red cod was caught on the south side of the peninsula than the north, but this difference was not statistically significant (mean difference: 14.02 g; 95% CI: -11.95 to 39.99).

ALONGSHORE

There were differences in red cod catch between the sites surveyed alongshore (Figure 4.16). Long Lookout had the greatest variability, but a significantly greater mass of red cod than Te Oka Bay (mean difference: 86.52 g; 95% CI: 10.50 to 106.05), and Decanter Bay (mean difference: 85.04 g; 95% CI: 30.84 to 139.24).

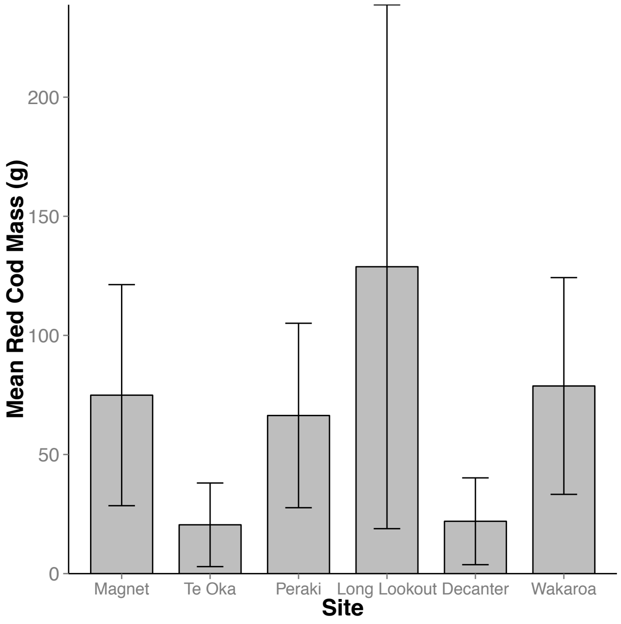

Figure 4.16: Mean mass of red cod caught per trap at each alongshore site with 95% CI.

HARBOUR

Within Akaroa Harbour, the total mass of red cod caught was broadly similar between each area, but changed substantially between seasons (Figure 4.17). Across the harbour the amount of red cod was greater in summer than in autumn (mean difference: 110.64 g; 95% CI: 68.23 to 153.03), winter (mean difference: 127.04 g; 95% CI: 84.65 to 169.42), and spring (mean difference: 130.57 g; 95% CI: 93.13 to 168.02).

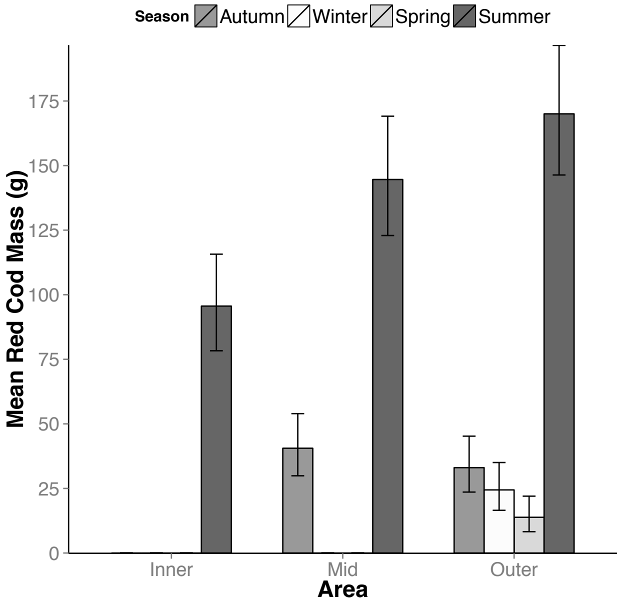

Figure 4.17: Mean mass of red cod caught per trap each season within the inner, mid, and outer areas of Akaroa Harbour with 95% CI.

4.3.4 Oceanography

Around the coast, a total of 197 CTD casts and secchi depth measurements were made over the course of the year. Within Akaroa Harbour 44 casts were conducted.

Temperature

OFFSHORE

Average surface water temperature around coastal Banks Peninsula was very similar between each distance from shore and side of the peninsula (Figure 4.18A). As expected, seasonal differences were present, but did not change between areas. Overall, water was warmer in summer than autumn (mean difference: 1.61 ºC; 95% CI: 1.05 to 2.16), winter (mean difference: 6.50 ºC; 95% CI: 5.94 to 7.06), and spring (mean difference: 3.07 ºC; 95% CI: 2.52 to 3.63). Bottom temperature results were very similar to those at the surface, with no notable differences between distances from shore or side of the peninsula, and similar trends between seasons (Figure 4.18B).

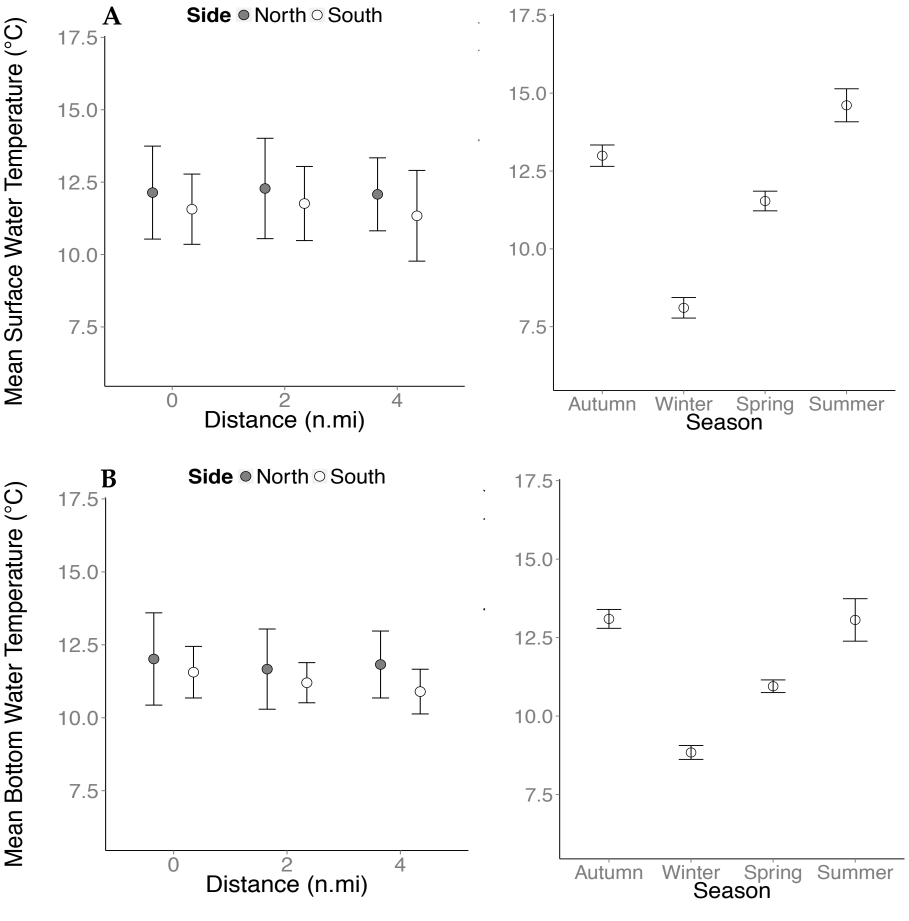

Figure 4.18: Mean surface (A) and bottom (B) water temperature around coastal Banks Peninsula for each distance from shore, side of the peninsula, and season with 95% CI.

ALONGSHORE

Surface temperature varied little among the alongshore sites and seasonal differences were comparable to those in Figure 4.18 at all sites. Decanter Bay in the North was slightly warmer than both Magnet Bay (mean difference: 0.61 ºC; 95% CI: 0.03 to 1.20), and Te Oka Bay (mean difference: 0.61 ºC; 95% CI: 0.03 to 1.20) in the South. There were no notable differences in bottom water temperature alongshore.

HARBOUR

Patterns in surface water temperature within Akaroa Harbour were very similar to those found around the coast (Figure 4.19A), with warmer water in summer than in autumn (mean difference: 3.22 ºC; 95% CI: 2.48 to 3.96), winter (mean difference: 8.72 ºC; 95% CI: 7.98 to 9.46), and spring (mean difference: 4.77 ºC; 95% CI: 4.12 to 5.42). Results were also very similar for bottom water temperature within the harbour (Figure 4.19B).

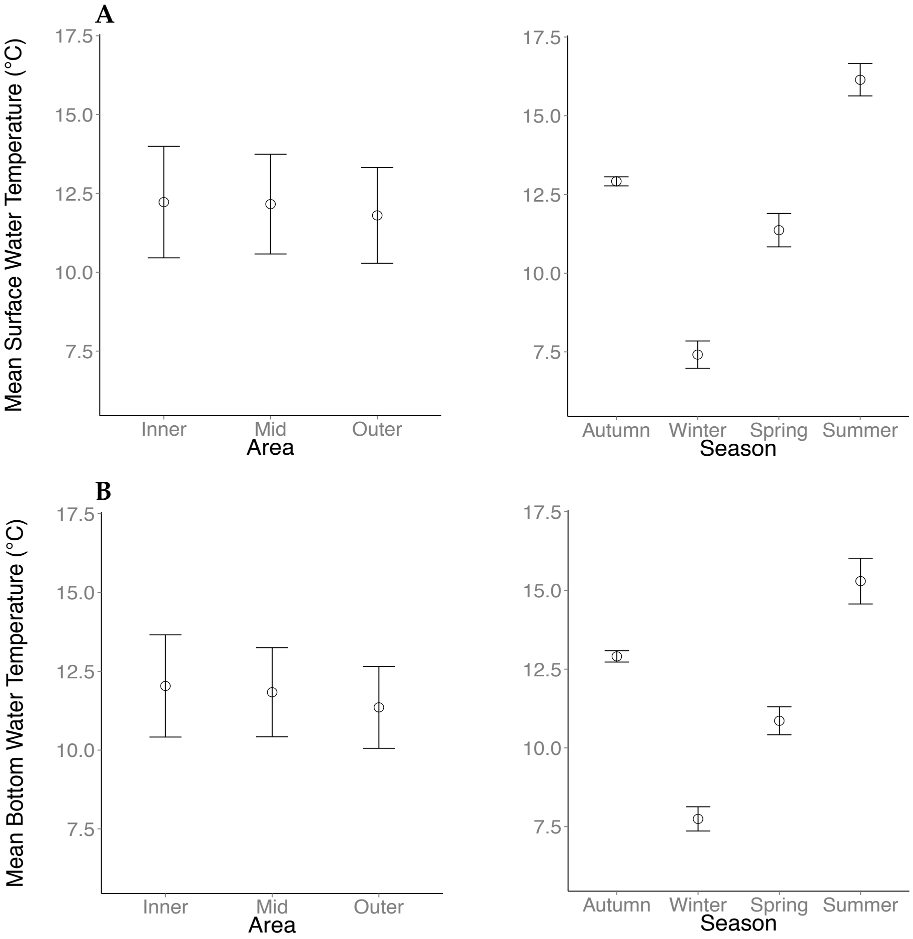

Figure 4.19: Mean surface (A) and bottom (B) water temperature in Akaroa Harbour for each area and season with 95% CI.

Salinity

OFFSHORE

Surface salinity around coastal Banks Peninsula differed between the north and south sides, depending upon distance from shore (Figure 4.20A). On average, it was lower on the south than the north, but only close to shore (0 n.mi; mean difference: -1.75 PSU; 95% CI: -2.25 to -1.24). On the south side, surface salinity was lower close to shore than at 2 n.mi (mean difference: -1.36 PSU; 95% CI: -1.87 to -0.85), and 4 n.mi (-1.40 PSU; 95% CI: -1.90 to -0.89). On the north, there were no clear differences between distances from shore. Seasonal differences were the same for all areas. On average, there was lower surface salinity in winter than both autumn (-0.98 PSU; 95% CI: -1.57 to -0.39) and summer (-1.10 PSU; 95% CI: -1.69 to -0.51). Similar trends were found for average bottom salinity (Figure 4.20B), with lower salinity at 0 n.mi from shore in the south (mean difference: -0.32 PSU; 95% CI: -0.09 to -0.55), and similar seasonal differences.

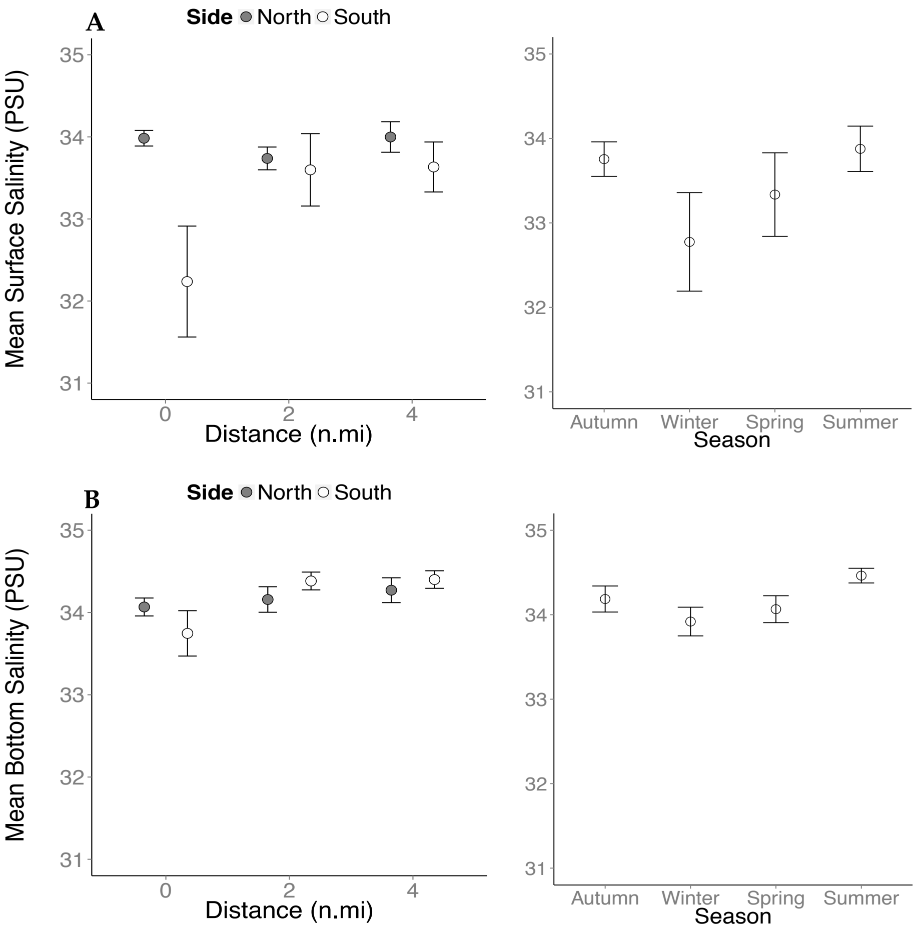

Figure 4.20: Mean surface (A) and bottom (B) salinity around coastal Banks Peninsula for each distance from shore, side of the peninsula, and season with 95% CI.

ALONGSHORE

Surface salinity differed among the sites surveyed alongshore. Sites on the north side of the peninsula all had greater surface salinity than those on the south. On the south side, Peraki Bay also had higher salinity than Magnet Bay (mean difference: 0.81 PSU; 95% CI: 0.14 to 1.49). Measurements of bottom salinity were lower at Magnet Bay than all sites surveyed on the north side. Seasonal differences were comparable to those presented in Figure 4.20 at all sites.

HARBOUR

There was a trend of increasing salinity towards outer Akaroa Harbour (Figure 4.21). Bottom salinity was significantly higher at the outer compared to the inner transect (mean difference: 0.26 PSU; 95% CI: 0.05 to 0.47). Seasonal trends were similar to coastal Banks Peninsula, with higher surface and bottom salinity in summer than autumn, winter, and spring.

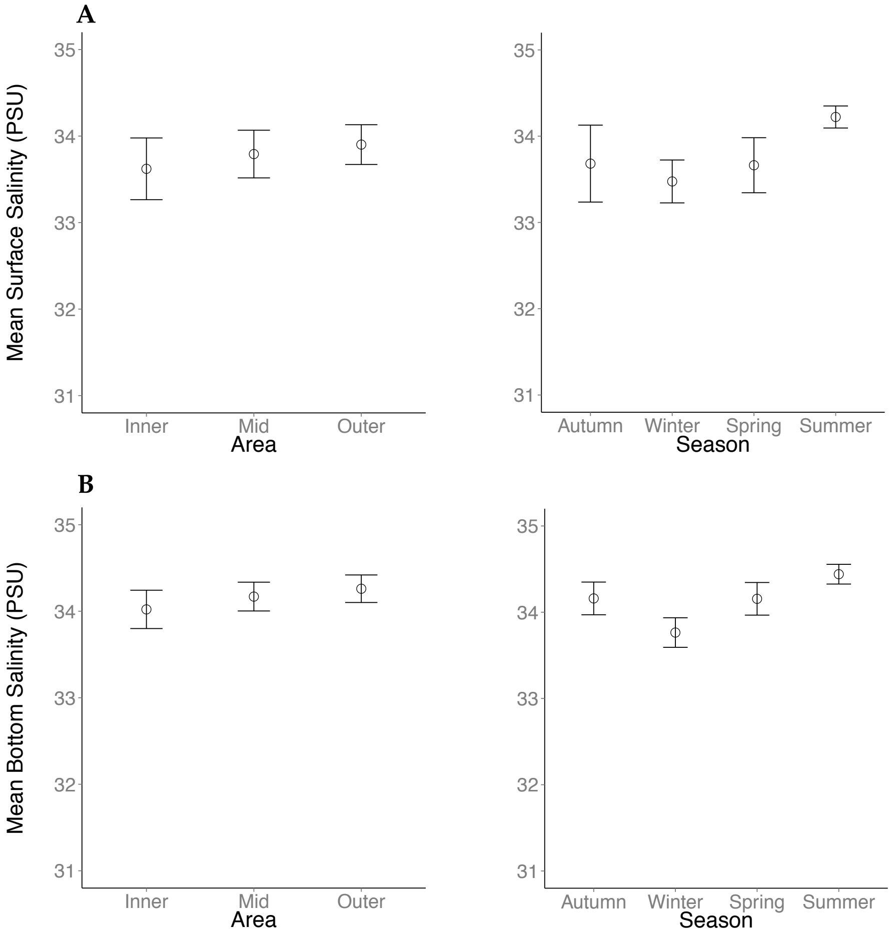

Figure 4.21: Mean surface (A) and bottom (B) salinity in Akaroa Harbour for each area and season with 95% CI

Chlorophyll a

OFFSHORE

Average surface chl *a* around coastal Banks Peninsula was slightly higher on the north side than the south (mean difference: 0.54 mg/m^3; 95% CI: 0.07 to 1.01) (Figure 4.22A). Distance from shore also affected results, with greater chl *a* closer to shore than at 2 n.mi (mean difference: 0.98 mg/m^3; 95% CI: 0.39 to 1.56), and 4 n.mi (mean difference: 0.82 mg/m^3; 95% CI: 0.26 to 1.38). Seasonal differences were consistent between areas. The largest difference was an increase in chl *a* in autumn compared to spring (1.27 mg/m^3; 95% CI: 0.61 to 1.94), and summer (0.70 mg/m^3; 95% CI: 0.03 to 1.38). Chl *a* near the sea floor significantly differed between the sides of the peninsula depending upon the distance from shore (Figure 4.22B). On average it was higher on the north side than the south, but only at 0 n.mi (mean difference: 2.72 mg/m3; 95% CI: 0.71 to 4.73), and 2 n.mi (mean difference 6.57 mg/m3; 95% CI: 4.63 to 8.51) from shore.

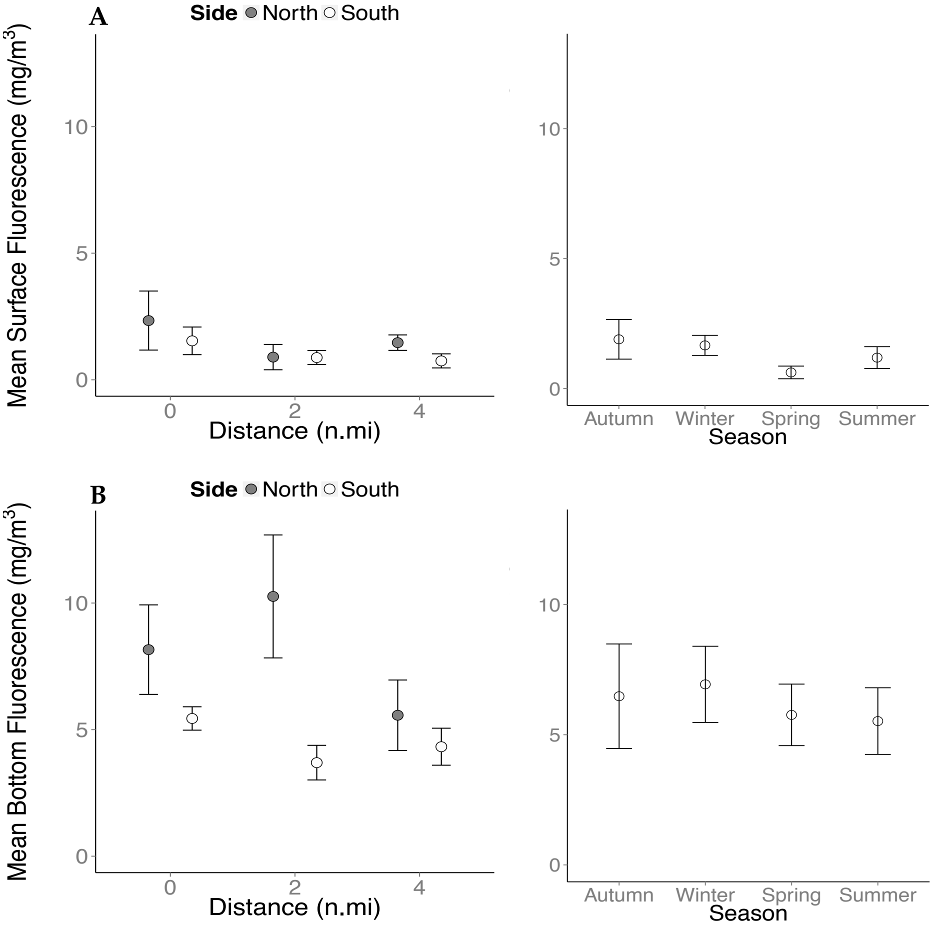

Figure 4.22: Mean surface (A) and bottom (B) chlorophyll *a* around coastal Banks Peninsula for each distance from shore, side of the peninsula, and season with 95% CI.

ALONGSHORE

The sites surveyed on the north and south sides of the peninsula differed in surface chl *a*, with higher measurements at Decanter and Wakaroa Bays in the north than both Magnet Bay (mean difference Decanter: 1.18 mg/m^3; 95% CI: 0.02 to 2.34; mean difference Wakaroa: 1.38 mg/m^3; 95% CI: 0.22 to 2.54), and Peraki Bay (mean difference Decanter: 1.17 mg/m^3; 95% CI: 0.01 to 2.32; mean difference Wakaroa: 1.36 mg/m^3; 95% CI: 0.20 to 2.52) in the south. Bottom chl *a* was higher at all sites surveyed on the north side than the south. Seasonal differences were comparable to Figure 4.22 at all sites.

HARBOUR

There were no significant differences in chl *a* detected between the areas of Akaroa Harbour (Figure 4.23). The most notable seasonal difference detected was an increase in surface chl *a* in summer compared to spring (mean difference: 2.14 mg/m^3; 95% CI: 0.98 to 3.29) and autumn (mean difference 2.33 mg/m^3; 95% CI: 1.02 to 3.63).

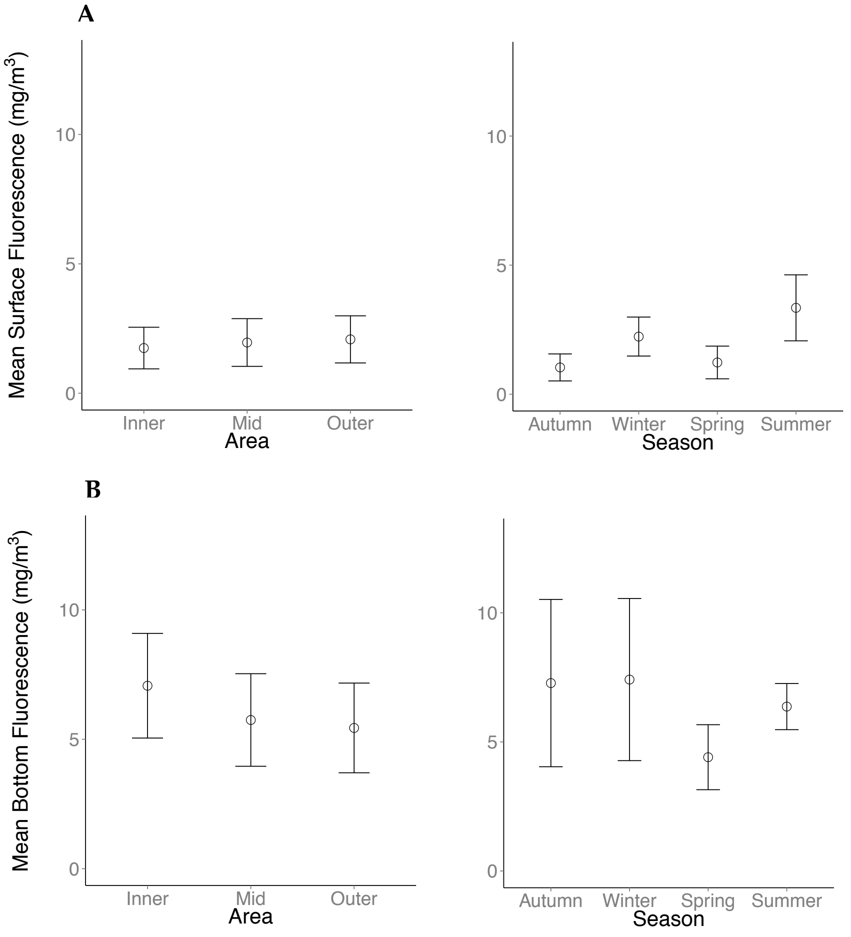

Figure 4.23: Mean surface (A) and bottom (B) chlorophyll *a* in Akaroa Harbour for each area and season with 95% CI

Clarity

OFFSHORE

Water clarity was similar between north and south sides of the peninsula. Unsurprisingly, clarity improved with increasing distance offshore and differed among seasons (Figure 4.24). At 4 n.mi from shore, water was clearer than both 0 n.mi (mean difference: 0.62 m; 95% CI: 0.28 to 0.96), and 2 n.mi (mean difference; 0.40 m; 95% CI: 0.06 to 0.73). Seasonal differences were consistent between each area. During both autumn and winter, clarity around the coast decreased compared to summer (mean difference autumn: -0.73 m; 95% CI: -1.07 to -0.38; mean difference winter: -0.58 m; 95% CI: -0.92 to -0.24), and spring (mean difference autumn: -0.55 m; 95% CI: -0.90 to -0.20; mean difference winter: -0.41 m; 95% CI: -0.76 to -0.05).

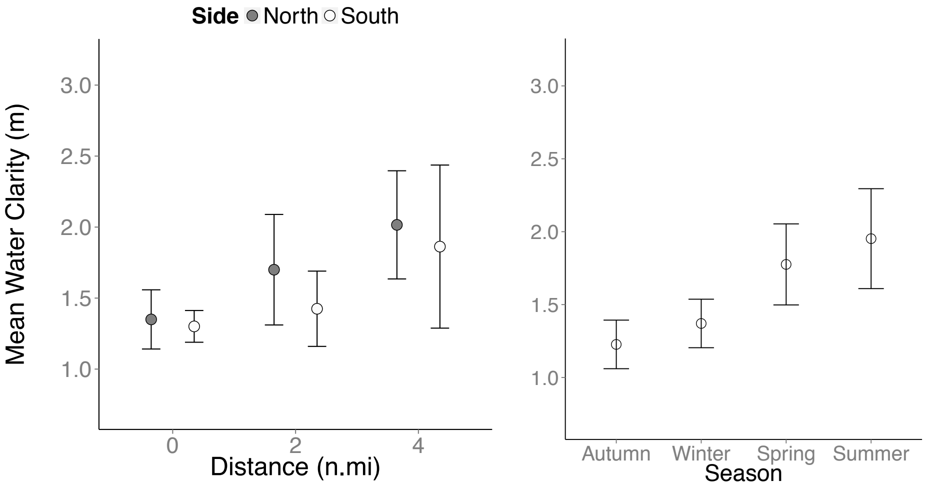

Figure 4.24: Mean water clarity around coastal Banks Peninsula for each distance from shore, side of the peninsula, and season with 95% CI.

ALONGSHORE

Water clarity differed among the alongshore sites, with clearer water at Decanter Bay than Magnet Bay (mean difference: 0.21 m; 95% CI: 0.002 to 0.41). Seasonal differences were comparable to those presented in Figure 4.24 at all sites.

HARBOUR

There were no notable differences between the three areas of Akaroa harbour (Figure 4.25). However, seasonal trends were evident, with the greatest difference being clearer water in autumn compared to winter (mean difference: 1.35 m; 95% CI: 0.60 to 2.09), and spring (mean difference 0.93 m; 95% CI: 0.26 to 1.59).

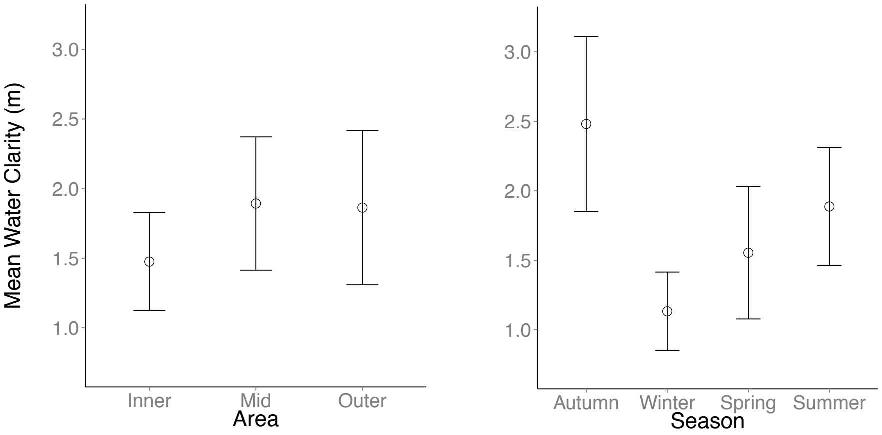

Figure 4.25: Mean water clarity in Akaroa Harbour for each area and season with 95% CI

4.3.5 Habitat model diagnostics & data exploration

There were no large outliers present in the data. Although there were several zero observations for the number of dolphins encountered, there was no evidence of zero-inflation. Tests for overdispersion confirmed this, with dispersion parameters of ϕ=0.71, ϕ=1.00, and ϕ=0.71 for the offshore, alongshore and harbour datasets respectively.

Pair plots of all predictor variables indicated no collinearity in any of the datasets for the three regions, with the majority of correlation coefficients falling between -0.3 and 0.3: the highest value of r=0.6 was between surface & bottom chl *a*. VIF values were all well below the acceptable level of 3 (Zuur et al. 2009a), ranging from 1.14 to 1.65, 1.17 to 2.43, and 1.22 to 1.96 for the offshore, alongshore and harbour datasets respectively.

Pair plots between the response variable and all predictor variables indicated slight non-linear patterns and high correlation between the number of dolphins and red cod mass for all three datasets (r=0.7 to 0.8), suggesting potential importance of this predictor variable in particular.

Residual plots of fitted values and all predictor variables for both the full GLM and GAM models of all three datasets indicated no strong patterns, validating the assumptions of homogeneity and independence.

4.3.6 Model comparison and selection

For each of the three study regions, a total of 15 models containing only oceanographic predictor variables were tested. Bottom temperature and salinity were not included in the models due to the similarity between trends in surface and bottom data for these variables (Section 4.3.4). Surface and bottom chl *a* were the most highly correlated predictor variables (r=0.6). While this correlation coefficient is not normally regarded as strong, I decided to exclude surface chl *a* from the models to remove any potential problems with collinearity. Surface chl *a* was excluded rather than bottom as this had the largest VIF value of the two. Three models containing only prey predictor variables were tested, comparing general prey indices (richness and diversity), data on red cod mass, and the two combined. A total of 45 models containing both oceanography and prey variables were then compared.

Offshore

For all offshore models, the GAMs had lower AIC and explained more deviance than their respective GLMs. The residual deviance of the best-fit offshore GAM was also found to be considerably lower than that of the best-fit GLM (Table 4.3). These results all suggest that incorporating non-linear effects through additive modelling improves model fit.

Table 4.3: Comparison of the best-fit GLM and GAM for the offshore dataset with predictor variables: surface salinity (Sal); bottom chlorophyll *a* (Chl) and red cod mass (RC).

	Model	**AIC**	**Deviance explained (%)**	**Residual deviance**
GLM	Dolp ~ Sal + Chl + RC	220.84	59.9	61.6
GAM	Dolp ~ s(Sal) + s(Chl) + s(RC)	208.38	70.9	44.7

All offshore GAMs within seven AIC points of the best-fit model are presented in Table 4.4.

Table 4.4: AIC and deviance explained for all offshore candidate GAMs with ΔAIC < 7. Predictor variables: surface salinity (Sal); bottom chlorophyll *a* (Chl); red cod mass (RC); surface temperature (Temp); clarity (Clar); richness (Rich); diversity (Div).

Model Predictor Variables	**AIC**	**ΔAIC**	**Deviance explained (%)**
s(Sal) + s(Chl) + s(RC)	208.38	0	70.9
s(Temp) + s(Sal) + s(Chl) + s(RC)	210.26	1.88	71.1
s(Clar) + s(Sal) + s(Chl) + s(RC)	210.33	1.95	70.9
s(Sal) + s(Chl) + s(Rich) + s(Div) + s(RC)	211.24	2.86	70.9
s(Temp) + s(Clar) + s(Sal) + s(Chl) + s(RC)	212.23	3.85	71
s(Chl) + s(RC)	212.89	4.51	67.4
s(Temp) + s(Sal) + s(Chl) + s(Rich) + s(Div) + s(RC)	213.11	4.73	71.1
s(Clar) + s(Sal) + s(Chl) + s(Rich) + s(Div) + s(RC)	213.19	4.81	70.9
s(Sal) + s(RC)	213.34	4.96	65.2
s(Temp) + s(Chl) + s(RC)	213.53	5.15	68.6
s(Clar) + s(Chl) + s(RC)	214.53	6.15	67.5
s(Temp) + s(Clar) + s(Sal) + s(Chl) + s(Rich) + s(Div) + s(RC)	215.07	6.69	71.1
s(Clar) + s(Sal) + s(RC)	215.17	6.79	65.7
s(Temp) + s(Sal) + s(RC)	215.18	6.8	65.2

None of the models containing only oceanographic predictor variables ranked within seven AIC points of the best-fit model. The model with surface temperature, salinity and water clarity as predictors was the best of all the oceanographic models tested, with an AIC of 252.99, explaining 47.7% of the deviance. With such models having a ΔAIC of >44.6 from the model with lowest AIC, there is relatively little support for using only oceanographic predictors when data on prey are available. This appears to hold true only if the prey data considered are specifically on species known to be important. All of the models in Table 4.4 included red cod mass as a predictor variable, while the prey model containing only general data on prey species richness and diversity had an AIC of 283.08 and explained only 26.5% of the deviance.

The top estimated models (Table 4.4) contain both red cod data and oceanographic variables however, indicating that this combination provides the best approximation of the relative abundance of Hector's dolphin, given the available data. Of these top models, those including both surface salinity and bottom chl *a* showed the most improvement in model fit. The addition of surface temperature, clarity, and general prey data increased the model complexity unnecessarily, as shown by the greater AIC scores of such models.

The best-fit model had the lowest AIC score of 208.38, explained 70.9% of the variance, and contained a total of 3 predictor variables, as outlined in Table 4.5.

Table 4.5: The best-fit GAM relating the offshore distributional patterns of Hector's dolphin at Banks Peninsula to oceanography and prey availability. Predictor variables: surface salinity (Sal); bottom chlorophyll *a* (Chl); red cod mass (RC).

Best-fit model:				
Dolp Ind ~ s(Sal) + s(Chl) + s(RC)				
Parametric Coefficient	**Estimate**	**SE**	***z*-value**	**p**
(Intercept)	0.278	0.113	2.452	0.014
Approx. significance of smooth terms	**edf**	**Ref. df**	χ^2	**p**
s(Surface salinity)	1.000	1.000	5.555	0.018
s(Bottom chlorophyll *a*)	1.798	2.245	7.830	0.026
s(Red cod mass)	2.437	2.978	85.349	<0.001
AIC: 208.38				
UBRE score: -0.238				
Deviance explained: 70.9%				

The relationship between each of these predictor variables and the response is presented by the smoothed curves in Figure 4.26.

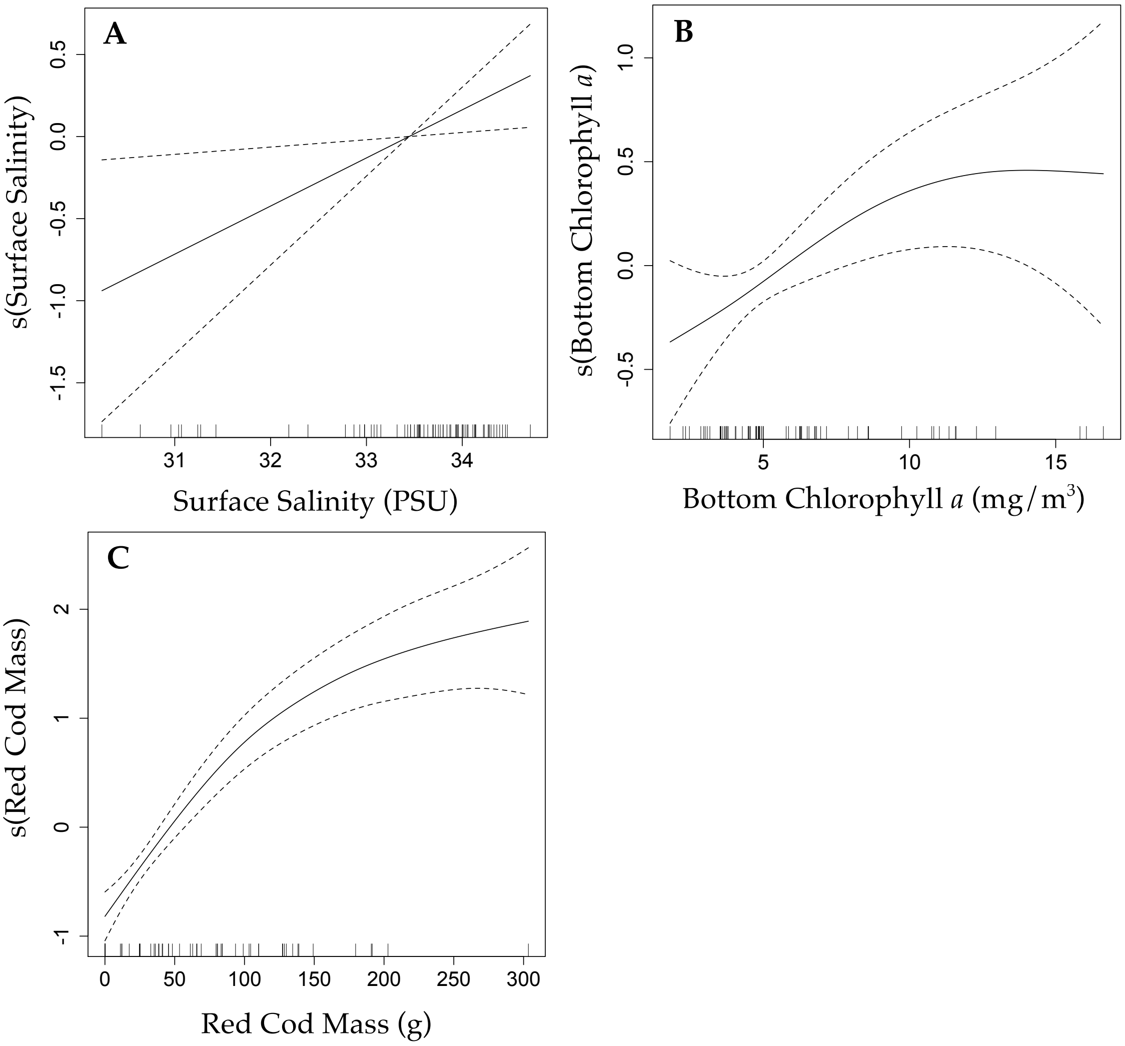

Figure 4.26: GAM results showing smooth functions of the relative abundance of Hector's dolphin in relation to each predictor variable of the best-fit offshore model: A) surface salinity; B) bottom chlorophyll *a*; C) red cod mass. Solid lines are the fitted models. Dashed lines are approximate 95% point-wise confidence intervals. Tick marks on the x-axis indicate the observations of that variable.

Surface salinity had a positive linear effect on the number of dolphins. There was also an increase in relative dolphin abundance with increasing red cod mass. When bottom chl *a* was greater than 10 mg/m^3, the number of dolphins encountered was relatively constant, decreasing in areas with lower chl *a*.

Alongshore

As with the offshore dataset, additive modelling was found to improve model fit. All GAMS had lower AIC and explained more deviance than their respective GLMs. The residual deviance of the best-fit alongshore GAM was also found to be considerably lower than that of the best-fit GLM (Table 4.6).

Table 4.6 Comparison of the best-fit GLM and GAM for the alongshore dataset with predictor variables: surface temperature (Temp); clarity (Clar); surface salinity (Sal); bottom chlorophyll *a* (Chl); diversity (Div) and red cod mass (RC).

	Model	**AIC**	**Deviance explained (%)**	**Residual deviance**
GLM	Dolp ~ Temp + Clar + Sal + Chl + Div + RC	250.83	60.3	129.8
GAM	Dolp ~ s(Temp) + s(Sal) + s(Chl) + s(Div) + s(RC)	194.16	85.3	47.9

All alongshore GAMs within seven AIC of the best-fit model are presented in Table 4.7.

Table 4.7: AIC and deviance explained for all alongshore candidate GAMs with ΔAIC < 7. Predictor variables: surface temperature (Temp); surface salinity (Sal); bottom chlorophyll *a* (Chl); diversity (Div); red cod mass (RC); clarity (Clar).

Model Predictor Variables	**AIC**	**ΔAIC**	**Deviance explained (%)**
s(Temp) + s(Sal) + s(Chl) + s(Div) + s(RC)	194.16	0	85.3
s(Temp) + s(Chl) + s(Div) + s(RC)	196.6	2.44	83.6
s(Temp) + s(Clar) + s(Chl) + s(Div) + s(RC)	197.14	2.98	84.5
s(Temp) + s(Clar) + s(Sal) + s(Chl) + s(Div) + s(RC)	199.21	5.05	84.5
s(Sal) + s(Chl) + s(Div) + s(RC)	200.9	6.74	82.7
s(Temp) + s(Sal) + s(Chl) + s(RC)	200.95	6.79	79.9

All of these models contained both oceanographic and prey predictor variables. The highest ranking model with only oceanographic data had ΔAIC of >82 from the model with lowest AIC. All of the top ranking models (Table 4.7) included red cod as a predictor variable, and all but one included data on prey diversity. Of the oceanographic variables, the addition of temperature and chl *a* appear to have the most improvement on model fit, being present in all models within five AIC of the best available model.

The best-fit model had the lowest AIC score of 194.16, explained 85.3% of the variance, and contained five predictor variables (Table 4.8).

Table 4.8: The best-fit GAM relating the alongshore distributional patterns of Hector's dolphin at Banks Peninsula to oceanography and prey availability. Predictor variables: surface temperature (Temp); surface salinity (Sal); bottom chlorophyll *a* (Chl); diversity (Div) and red cod mass (RC).

Best-fit model:				
Dolp ~ s(Temp) + s(Sal) + s(Chl) + s(Div) + s(RC)				
Parametric Coefficient	**Estimate**	**SE**	***z*-value**	**p**
(Intercept)	-0.571	0.488	-1.169	0.242
Approx. significance of smooth terms	**edf**	**Ref. df**	χ^2	**p**
s(Surface temperature)	4.263	4.937	21.917	<0.001
s(Surface salinity)	6.971	6.996	18.895	0.009
s(Bottom chlorophyll *a*)	3.068	3.735	14.590	0.005
s(Prey diversity)	1.000	1.000	7.135	0.008
s(Red cod mass)	3.288	3.986	88.571	<0.001
AIC: 194.16				
UBRE score: 0.281				
Deviance explained: 85.3%				

The relationship between each of these predictor variables and the response is presented by the smoothed curves in Figure 4.27.

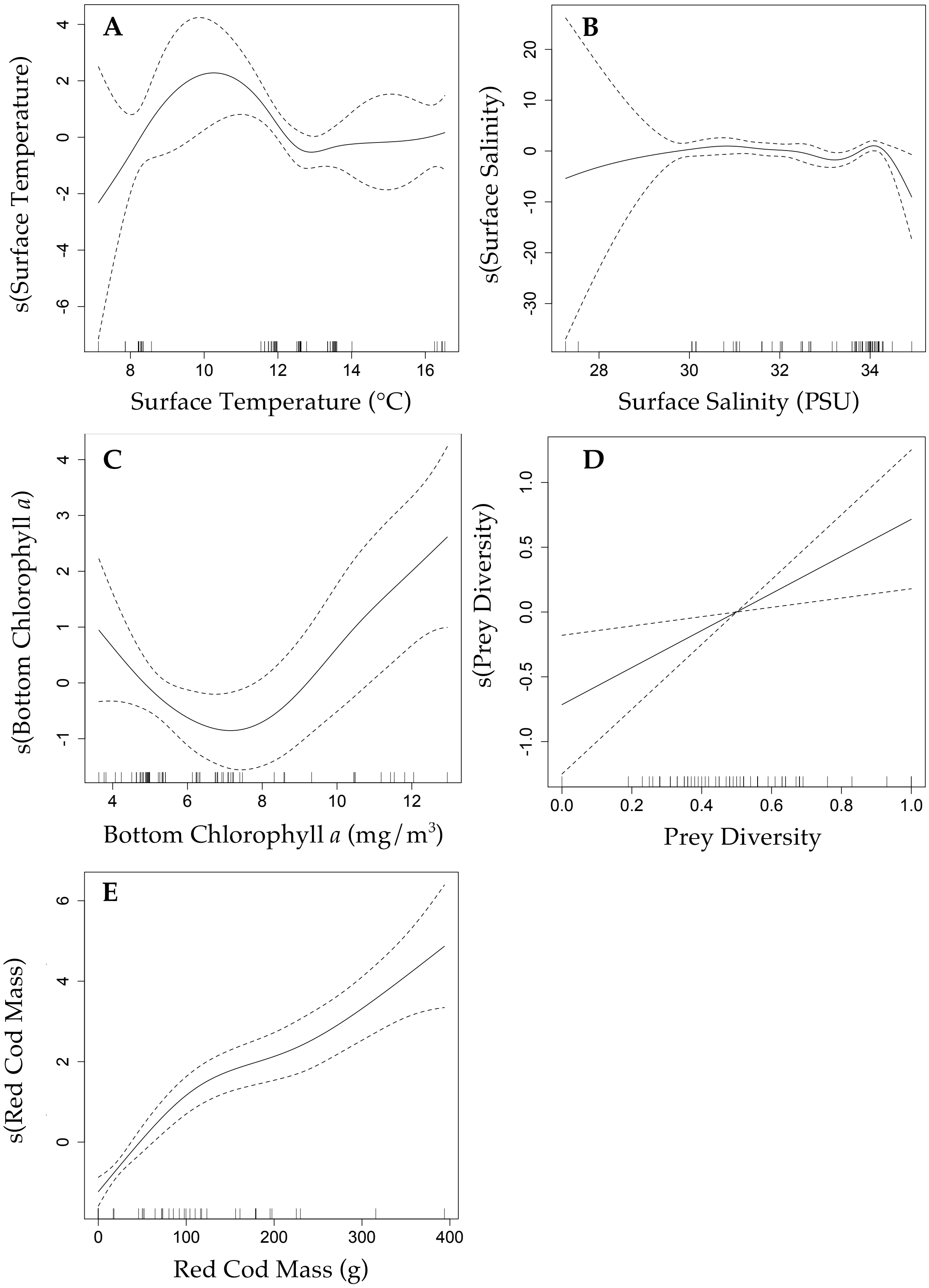

Figure 4.27: GAM results showing smooth functions of the relative abundance of Hector's dolphin in relation to each predictor variable of the best-fit alongshore model: A) surface temperature; B) surface salinity C) bottom chlorophyll *a*; D) prey diversity; E) red cod mass. Solid lines are the fitted models. Dashed lines are approximate 95% point-wise confidence intervals. Tick marks on the x-axis indicate the observations of that variable.

It initially appears that relative dolphin abundance was greatest between surface temperatures of 8 and 12 °C, however the lack of data points between these temperatures suggests that this may be over-fitted. Without this spike abundance appears to increase very slightly with increasing temperature. In terms of salinity, the number of dolphins peaked at 34 PSU. Encounter rate was lowest when bottom chl *a* was between 5 and 8 mg/m^3, increasing with greater chl *a*. There was a positive linear effect of prey diversity, and an increase in dolphin encounters with increasing red cod mass.

Harbour

Once again additive modelling improved model fit, with all GAMs resulting in lower AIC scores and explaining more deviance than the respective GLMs. The residual deviance of the best-fit harbour GAM was also considerably lower than that of the best-fit GLM (Table 4.9).

Table 4.9: Comparison of the best-fit GLM and GAM for the harbour dataset with predictor variables surface temperature (Temp); clarity (Clar) and red cod mass (RC).

	Model	**AIC**	**Deviance explained (%)**	**Residual deviance**
GLM	Dolp ~ Temp + Clar + RC	101.76	61.8	41.00
GAM	Dolp ~ s(Temp) + s(Clar) + s(RC)	96.74	79.8	21.71

All harbour GAMs within seven AIC of the best-fit model are presented in Table 4.10. All but one of the best models contained both oceanographic and prey predictor variables. Red cod mass was included in all of these models. Of the oceanographic variables, water temperature appeared to contribute most to model fit. Overall, the change in AIC between many of the harbour models was smaller than that of the offshore or alongshore models, resulting in the greater number of models presented in Table 4.10.

Table 4.10: AIC and deviance explained for all harbour candidate GAMs with ΔAIC < 7. Predictor variables: surface temperature (Temp); clarity (Clar); red cod mass (RC); bottom chlorophyll *a* (Chl); surface salinity (Sal); diversity (Div).

Model Predictor Variables	**AIC**	**ΔAIC**	**Deviance explained (%)**
s(Temp) + s(Clar) + s(RC)	96.74	0	79.8
s(Temp) + s(RC)	97.15	0.41	71.9
s(Temp) + s(Chl) + s(RC)	97.29	0.55	74.2
s(Temp) + s(Clar) + s(Sal) + s(RC)	98.46	1.72	80
s(Temp) + s(Sal) + s(RC)	98.59	1.85	72.7
s(Temp) + s(Clar) + s(Div) + s(RC)	98.61	1.87	79.7
s(Temp) + s(Div) + s(RC)	98.84	2.1	72.2
s(Temp) + s(Sal) + s(Chl) + s(RC)	99.22	2.48	74.2
s(Temp) + s(Sal) + s(Chl) + s(RC)	99.23	2.49	74.2
s(Clar) + s(RC)	99.78	3.04	79.1
s(Temp) + s(Clar) + s(Sal) + s(Chl) + s(RC)	100.14	3.4	80
s(Clar) + s(Chl) + s(RC)	100.17	3.43	76.1
s(Temp) + s(Clar) + s(Chl) + s(RC)	100.19	3.45	76.1
s(Temp) + s(Clar) + s(Chl) + s(Div) + s(RC)	100.32	3.58	79.7
s(Temp) + s(Clar) + s(Sal) + s(Div) + s(RC)	100.34	3.6	80.1
s(Temp) + s(Sal) + s(Div) + s(RC)	100.37	3.63	72.9
s(Temp) + s(Sal) + s(Chl) + s(Div) + s(RC)	101.17	4.43	74.2
s(Clar) + s(Sal) + s(RC)	101.61	4.87	79.1
s(Clar) + s(Chl) + s(Div) + s(RC)	101.88	5.14	76.4
s(Clar) + s(Sal) + s(Chl) + s(RC)	101.99	5.25	76.3
s(Temp) + s(Clar) + s(Sal) + s(Chl) + s(Div) + s(RC)	102.03	5.29	80.1
s(RC)	102.04	5.3	63.2
s(Chl) + s(RC)	102.59	5.85	66.8

The best-fit model had the lowest AIC score of 96.74, explained 79.8% of the variance, and contained three predictor variables (Table 4.11).

Table 4.11: The best-fit GAM relating the distributional patterns of Hector's dolphin in Akaroa Harbour to oceanography and prey availability. Predictor variables: surface temperature (Temp); clarity (Clar); red cod mass (RC).

Best-fit model:				
Dolp ~ s(Temp) + s(Clar) + s(RC)				
Parametric Coefficient	**Estimate**	**SE**	***z*-value**	**p**
(Intercept)	-0.820	0.304	-2.70	0.007
Approx. significance of smooth terms	**edf**	**Ref. df**	χ^2	**p**
s(Surface temperature)	4.657	5.479	13.027	0.032
s(Clarity)	2.974	3.577	4.077	0.330
s(Red cod mass)	2.502	2.956	13.632	0.003
AIC: 96.74				
UBRE score: -0.001				
Deviance explained: 79.8%				

The relationship between each of these predictor variables and the response is presented by the smoothed curves in Figure 4.28. There was a peak in dolphin relative abundance between surface temperatures of 10 and 15 °C with a general increasing trend in abundance as temperature increases. Dolphin abundance was also slightly higher in areas of lower water clarity, though this factor was not indicated as statistically significant in Table 4.11. The number of dolphin encounters increased with greater red cod mass up to catches of approximately 200 g.

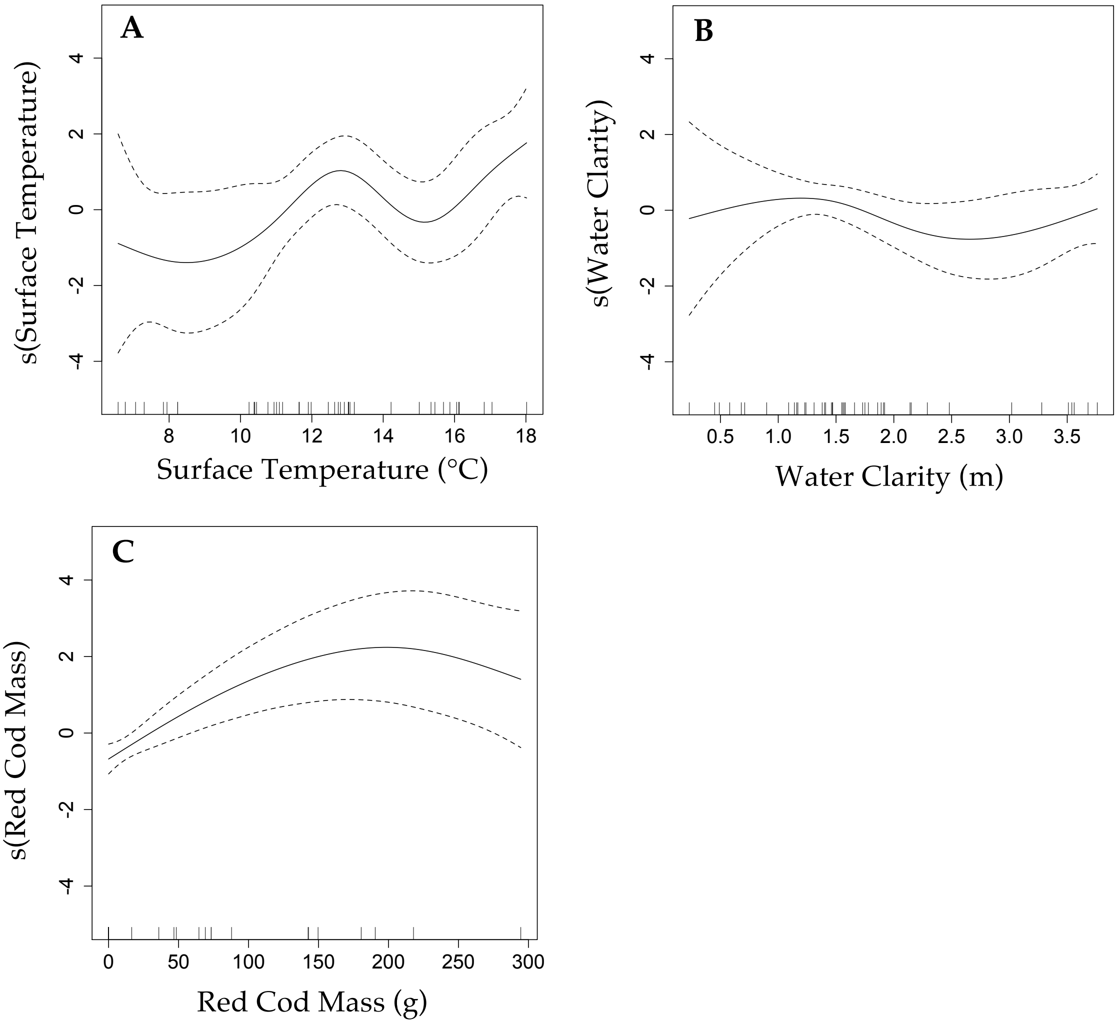

Figure 4.28: GAM results showing smooth functions of the relative abundance of Hector's dolphin in relation to each predictor variable of the best-fit harbour model: A) surface temperature; B) water clarity C) red cod mass. Solid lines are the fitted models. Dashed lines are approximate 95% point-wise confidence intervals. Tick marks on the x-axis indicate the observations of that variable.

4.4 DISCUSSION

By concurrently sampling Hector's dolphin relative abundance, important prey species, and the oceanography of the surrounding water column, it was possible to identify a suite of predictors which show strong relationships with dolphin distribution. Seasonal changes in dolphin distribution away from shore were similar to those previously recorded (Rayment et al. 2010), with more sightings close to shore and fewer further from shore in warmer months. Within Akaroa Harbour, an increase in dolphin numbers was found in the inner harbour during summer, as in Dawson et al. (2013b). A dissimilarity with that study however, was the apparently lower number of dolphins in the outer harbour in all other seasons.

Seasonal patterns in red cod mass were similar to those of dolphin distribution in all three regions and this correlation is reflected by the strong influence of this parameter in the best fitting models. Red cod were found to contribute most in terms of mass to the dolphins' diet in Chapter 2 (Miller et al. 2013). From these modeling results, it seems that as an important prey species, red cod also contribute to driving the dolphins' distribution patterns. Trawl surveys are not usually carried out at such a small scale in the near-shore waters where Hector's dolphins are most often encountered (Beentjes et al. 2002). Nevertheless, red cod are known to migrate into shallow inshore waters in warmer months (Paul 2000), and my results support this. During summer and autumn they feed extensively on squat lobster (*Munida gregaria*), which occur in large shoals throughout bays and harbours at that time (Carter and Malcolm 1926) and were sighted on several occasions during this study.

Overall, the parameters of the three best fitting GAMs explained a relatively large amount of variation in dolphin distribution. Both oceanographic and prey parameters contributed to the final models for each region, indicating that there is value in collecting and using both types of data in combination. All of the GAMs within 7 AIC points of the best model, included red cod mass as a predictor variable. The prevalence of this predictor above all others indicates that this variable in particular, is highly correlated with dolphin distribution, as was shown by the strong correlation coefficients during data exploration (r=0.7 to 0.8).

Patterns in offshore distribution suggest a preference for areas of higher chl *a* and surface salinity, and a greater mass of red cod. Data exploration revealed that chl *a* around Banks Peninsula was slightly higher on the north side and closer to shore, salinity was lower in winter months, and patterns in red cod mass matched patterns in dolphin distribution across both areas and seasons.

Patterns in dolphin distribution alongshore suggest a preference for areas of higher chl *a,* higher surface salinity, and slightly warmer SST. Relative abundance was again higher in areas of greater red cod mass, as well as higher prey diversity. Data exploration revealed that all of these factors tended to be higher in bays on the north side of the peninsula than the south. Red cod mass closely matched the trend in dolphin distribution, with greater values at Long Lookout Point in particular. The combination of conditions in this area appear to make it a hotspot for Hector's dolphins. While Clement (2005) did not survey Long Lookout Point, the bays just to the east were found to be a generalised hotspot, regularly occupied by Hector's dolphins over most of the year. Rayment et al. (2010), also reported a high number of sightings in this area during summer aerial surveys.

Areas of higher chl *a* are indicative of higher productivity, which explains why the increased chl *a* in the northern and inshore areas coincided with a higher mass of red cod. The higher productivity in these regions would support prey items of red cod, and subsequently carry up through the food chain, leading to areas of greater dolphin abundance. Higher productivity can be indicative of coastal upwelling events, when wind-water interaction brings dense, nutrient-rich water up to the surface (Franks 1992). Previous work around the coastal Canterbury region has found upwelling to be driven by northerly winds (Heath 1972a, b). Bays on the north and east sides of Banks Peninsula are directly exposed to weather from the north, while the Peninsula's steep cliffs and elevation create a wind-break for the southern bays. In late spring and summer, winds and swell from the north are most frequent, resulting in higher incidents of upwelling (Heath 1972a, b, Carter and Herzer 1979). Oceanographic studies by Clement (2005) found upwelling events to be more common on north-eastern Banks Peninsula, while southerly winds and large river outflows resulted in frequent transport of cooler, offshore waters into inshore regions (*i.e.* downwelling) in the south (Figure 4.1). Due to the greater outflow from rivers, the Canterbury Bight to the south also has lower salinity than Pegasus Bay to the north (Figure 4.1). This corresponds to my observations of higher surface salinities in the northern bays.

Patterns in distribution throughout Akaroa harbour were linked to a preference for areas of higher red cod mass. There is also a suggestion of preference for areas of warmer SST. The similarity in water temperature between all areas of the harbour however, indicates that this factor is most likely an artefact of seasonal variation, with warmer water in summer when dolphins are more likely to be present. During cooler months, dolphins were rarely sighted in any areas of the harbour or any of the other alongshore sites, and were instead more often present at the transect 4 n.mi from shore. As SST was not warmer further from shore during these months, I suspect that the dolphins are not directly selecting habitat based upon temperature in this region. Bräger et al. (2003) also doubted that winter SST further from shore is any warmer than inshore areas, and believed that seasonal shifts in Hector's dolphin distribution were almost certainly related to changes in food supply.

Habitat models of the closely related Chilean dolphin (*Cephalorhynchus eutropia*) revealed association with areas of slightly warmer water and reduced clarity (Heinrich 2006). It was concluded however, that this is most likely a secondary result of their preference for shallow-water habitats and prey distribution, rather than active selection of these features (Heinrich 2006). The same has been suggested for humpback dolphins and their indirect association with turbid waters (Karczmarski et al. 2000).

The results suggest that data on prey species of known importance are more valuable than general indices of potential prey abundance. Therefore, knowledge of a species' dietary preferences is useful in selecting parameters that may be ecologically meaningful. Hector's dolphins were found to eat a relatively wide range of species in Chapter 2 (Miller et al. 2013), indicating that they feed throughout the water column. It may be that other prey species play an important role in influencing the dolphins' movements, particularly in other populations. Differences were found between the diets of dolphins from the South Island east and west coasts (Miller et al. 2013). Red cod occurred in a greater percentage of the stomachs examined from the east coast, and in general a greater number of demersal species were eaten in this area. Several of the other identified prey species which were beyond the scope of sampling in this study, including flounder (*Rhombosolea plebeia*; Paul 2000), yelloweyed mullet (*Aldrichetta forsteri*; Paul 2000), and arrow squid (*Nototodarus sloanii*; McKinnon 2007), are also known to move inshore during the warmer months.

There is considerable scope to extend this study in the future, by surveying the seasonal availability of additional prey species, both around Banks Peninsula and within other populations. Stable isotope analysis of dolphins from Banks Peninsula (Chapter 3), suggested that epipelagic bony fish, such as pilchard, contribute most to the dolphins diet over the long term, while red cod contributed most in the seasonally-biased stomach contents. Surface feeding has been observed on several occasions throughout the year in this study and by others (e.g. Bräger 1998), on small fish such as sprat and yelloweyed mullet. As my study focussed on sampling demersal prey, the use of alternative fishing methods, such as surface trawls and active acoustics, should be considered in future studies, to survey species from additional habitats. Surveys of epipelagic schooling fish may also require sampling of additional temporal scales, to examine the predictability and persistence of prey patches (Redfern et al. 2006).

The traps used in this study present inherent sampling biases, as does any sampling method. They were designed based upon the success of similar studies (Whitelaw et al. 1991, Sheaves 1995, Willis and Babcock 2000) and aimed to capture demersal species of a similar size range to that eaten by Hector's dolphins (Miller et al. 2013). Only those species attracted to the bait or trap itself, and inclined to enter the funnels, could be sampled however, and so several demersal species, such as flatfish, were unlikely to be caught. This is important to keep in mind, and highlights the need to test potential sampling methods to ensure the results fit the aims of the study. As red cod were frequently caught during trial deployments of these traps, the results were deemed suitable to assess habitat use in relation to an important prey species. In Chapter 5, I consider an alternative method for surveying prey, by comparing results from concurrent fish trap and baited stereo-video deployments. Stereo-video systems have several potential advantages over using traps. They do not require species to be captured in order to sample them, and can provide accurate and precise measurements that are objective and unbiased (Harvey and Shortis 1995, Shortis and Harvey 1998). The initial set-up of such systems can be costly, however, and reviewing video-footage can be time-consuming (Shortis et al. 2013).

To strengthen the predictive capacity of these models, future work should extend the spatial and temporal scale of this study (Redfern et al. 2006). It will be important to collect data over additional years, to account for year-year variation, and sample additional locations. Habitat selection described by Bräger et al. (2003) was found to differ between the east and west coast populations. Diurnal movement of Hector's dolphins within Akaroa harbour has been found through acoustic monitoring, and the distribution of prey is thought to be the major driver of these movement patterns

(Dawson et al. 2013b). While no data on prey have been collected within Akaroa harbour at this smaller temporal scale, diurnal movements of prey species have been documented in another harbour environment by Morrison et al. (2002), including yelloweyed mullet, sole (*Peltorhamphus* sp.), flounder, and anchovy (*Engraulis australis*).

Another potentially important driver to consider in future habitat models is predation risk. Further research is needed to determine the nature and extent of this risk, and identify areas which would provide refuge. Heithaus and Dill (2002) found that bottlenose dolphin habitat selection in Shark Bay, Western Australia, was driven by a trade-off between prey availability and predation risk from sharks. Injuries from shark bites, most probably from other shark species, are occasionally seen on living Hector's dolphins. While Hector's dolphin remains have been found in the stomachs of seven-gill sharks (Cawthorn 1988, Slooten and Dawson 1994) it is unknown whether this resulted from predation (while alive) or scavenging (after death). There are no written records of predation on Hector's dolphins by killer whales (Jefferson et al. 1991), though clear avoidance of killer whales by Hector's dolphins has been observed at Banks Peninsula (Dawson, unpub. obs.). It is also possible that wave exposure may influence Hector's dolphins movements, with selection for more sheltered areas during calving to reduce energetic requirements (Wilson et al. 1997). This is unlikely however, as the stronghold for this species is on the South Island west coast, which is comparatively very exposed.

Conclusion

These models present the first attempt to associate Hector's dolphin habitat use with data on both oceanography and prey availability. They were able to identify factors that account for a relatively high amount of the variation in habitat use throughout three regions. The best-fitting models for all three regions indicated that a combination of data on oceanographic factors and the mass of an important prey species, red cod, best describe the patterns in Hector's dolphin distribution. Expansion of this work to include additional temporal and spatial scales, will further strengthen the predictive capacity of these models for nationwide identification of important habitat, and areas with potential for population recovery and expansion.

CHAPTER 5

AN ALTERNATIVE METHOD FOR SURVEYING PREY: A COMPARISON OF REMOTE STEREO-VIDEO AND TRAP METHODS FOR ASSESSMENT OF DEMERSAL PREY AVAILABILITY AT BANKS PENINSULA

5.1 INTRODUCTION

Mid trophic level marine organisms serve as an important link between lower trophic species (*i.e.* plankton) and top-predators. Many birds, fish, and marine mammals rely on mid-trophic planktonic feeding fish as their main source of prey, and as such, these species are critical to ecosystem function. Many management issues require an understanding of changes in top predator populations, under the increasing pressures of fishing and climate change. Surveying mid-trophic organisms is a key step in linking oceanographic processes to the population dynamics of large pelagic predators.

Assessing distribution and abundance accurately can be challenging, particularly in marine environments where making observations is difficult, and estimates are often influenced by the chosen sampling methods. Each method has its own inherent biases that must be borne in mind when drawing conclusions. Comparisons between methods can help identify relative biases and differences in species detectability. Two main categories of sampling methods exist: capture methods and observational methods. The goal of this chapter is to compare a method from each of these categories in sampling Hector’s dolphin prey availability around Banks Peninsula.

Trapping is commonly used in surveys of fish assemblages (e.g. Recksiek et al. 1991, Whitelaw et al. 1991, Sheaves 1995, Heithaus 2004). The design of traps varies, though the basic principle is the same. Species are captured by entering through funnels, which narrow towards the inner end inhibiting escape. Species may be attracted to traps as a form of cover or protection, though bait is often used to lure species. Traps are often favoured as they are a form of non-destructive sampling – they allow fish to be successfully released alive, potentially to be caught again. Traps can also sample topographically complex seabeds that would snag trawls and other net-based methods, and can be used at any depth. They can also be left unattended for short or long periods of time, and are typically robust and inexpensive. They may be bulky to transport however, and there are several biases in their sampling capability. Catch rates vary for different species depending on attributes such as mesh size (Sheaves 1995, Robichaud et al. 1999, Mahon and Hunte 2002), and conspecific attraction or predation may occur (Munro 1974). Observational methods such as SCUBA and video have been used in conjunction with trapping surveys to improve trap design (Jury et al. 2001, Renchen et al. 2012).

The use of underwater video to sample marine species has increased in recent years with advances in technology (e.g. Harvey and Shortis 1995, Watson et al. 2005, Mueller et al. 2006, Heagney et al. 2007). Stereo-video techniques can augment estimates of relative species abundance and diversity with accurate and precise measurements (Harvey and Shortis 1995, Petrell et al. 1997, Shortis and Harvey 1998, Harvey et al. 2001, 2003). Measurements from scale bars or lasers in single-video systems can provide coarse estimates of length, but are substantially less accurate and precise than stereo-video (Willis and Babcock 2000, Harvey et al. 2002b), and are necessarily 2-D, rather than 3-D as offered by stereo-video.

Remote stereo-video systems are commonly deployed fixed to a frame that rests on or near the seafloor (e.g. Harvey and Shortis 1995, Cappo et al. 2003, Watson et al. 2005). Such systems can be deployed at depth and over a wide variety of habitat types (Shortis et al. 2007, Althaus et al. 2009, Merritt et al. 2011). Typical disadvantages of such systems, however, are that the initial set up cost can be relatively high, and reviewing video footage can be time-consuming (Shortis et al. 2013). Potential sampling biases include the possible underestimation of abundance or size (Harvey et al. 2012) as species counts and measurements can only be made from the maximum number of fish sighted in a single video frame (Willis and Babcock 2000). Video sampling is also profoundly influenced by water clarity, and bait is often used to attract species to within the field of view (Watson et al. 2005, Harvey et al. 2007).

Few studies have compared the use of traps and baited video systems. Those that have, have found differences in the species and sizes of fish sampled. Harvey et al. (2012) concluded that stereo-video may be a more versatile sampling tool than traps alone, with video recordings sampling a higher number and diversity of species, and a wider range of fish lengths than traps. Similarly, Bachelor et al. (2013) reported that reef fish were observed much more frequently on video footage than within traps. Priede et al. (2009) found that baited video was able to sample very small individuals that were able to escape through the mesh of capture gear, while Wells et al. (2008b) showed that traps sampled larger fish than a video array. The aim of this work is to compare these two methods for sampling small, demersal prey of Hector's dolphins at Banks Peninsula. The species and sizes sampled by each technique are compared, and the logistics and performance of each method are discussed.

5.2 METHODS

5.2.1 Sampling Equipment

Trap design

To sample potential prey availability I used a circular trap (Figure 5.1).

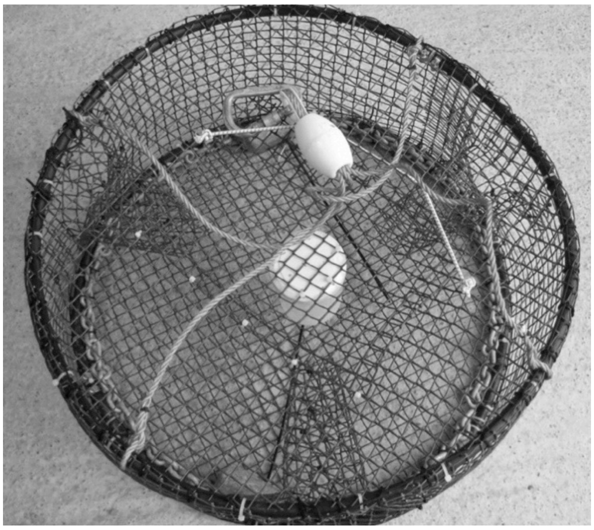

Figure 5.1: Trap design.

As described in Chapter 4, the trap measured 70 cm in diameter and 30 cm in height. Bottom, top, and sides were made of semi-rigid plastic mesh with holes about 1 cm x 1 cm. Three mesh funnels were located on the sides of the trap, leading towards the bait in the centre. Trap size was limited by the space on the research vessel. Similar fish surveys have found that catch rate does not generally increase with trap size, however. Sheaves (1995) for example, found that larger traps caught more fish for only one of 22 species, and so recommended smaller traps for their practicality.

Each trap was set on the seafloor with 6kg of weight and a small 2 kg danforth anchor to stop it being dragged by the tide. A clip at the top attached the trap to a nylon rope and surface buoy for easy retrieval. I used approximately 200 g of thawed, chopped pilchard as bait because of its high oil content and proven effectiveness in similar fish surveys (e.g. Willis and Babcock 2000). The bait was contained in a plastic jar with numerous small holes. Such a design has been found to give the highest catch rate and allow bait to last longer (Sheaves 1995).

Stereo-video design

The stereo-video system design was based on previous systems that aimed to sample large reef fish (Harvey and Shortis 1995, Merritt et al. 2011). As my study aimed to sample relatively smaller fish (less than 60 cm in length) in relatively poorer visibility than these previous studies, the system was reduced in size so as to focus on recording a smaller area closer to the cameras. The system I used in this study included two Canon Legria HF200 high definition (1920x1080 pixels) camcorders with 0.66x wide angle lenses. I chose this camcorder model as it is capable of progressive recording, which increases the precision of measurements made from individual video frames, and it records to flash memory, which is more robust than hard disk drive. Thirty-two gigabyte Class 4 SD cards and Canon BP-827 batteries were used to record for the full length of deployment at maximum resolution. When the system was designed, this camcorder model also provided the best specifications in terms of focal length and sensor size, and the largest field of view. The focal length of each camcorder was set to 4.1 mm to obtain fields of view of 0.94 m at a range of 1 metre.

The camcorders were fixed within PREVCO Subsea PVC underwater housings, mounted on a 80 cm wide stainless steel frame (Figure 5.2) with a camcorder base separation of 55 cm.

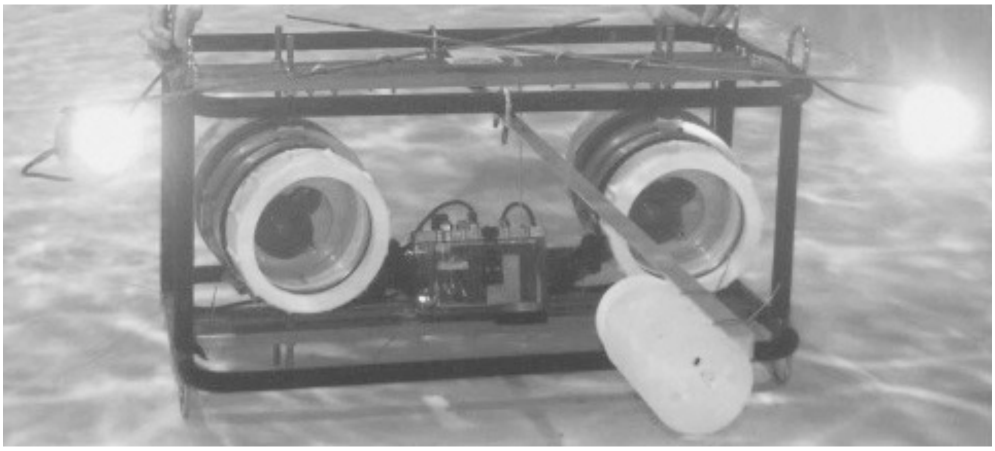

Figure 5.2: Stereo-video system.

The camcorders were each inwardly converged at 8° to gain an optimised field of view. The optically clear acrylic endcaps of the housings were modified with connectors to allow the camcorders to be downloaded and charged without moving them or opening the housing. I also started and stopped recordings remotely to avoid opening the housings on deployment and retrieval. This greatly improved the stability of the system as the relative position of the camcorders was not changed between recordings.

A removable bait bar was clamped to the middle of frame before deployment (Figure 5.2) so that it was within the field of view of both camcorders, at approximately 60 cm distance. At the start of each deployment, I filled the bait jar with ~ 200 g of thawed chopped pilchard, as was the case with the trap. A calibration check-plate was built onto the lid of the bait jar, with points at a known distance apart to verify the stability of the relative orientation of the camcorders (Harvey and Shortis 1995). Two 3 watt (270 lumens) white halogen lights moulded in waterproof resin housings were mounted at either side of the frame (Figure 5.2) and powered by a battery housing secured to the frame's centre.

The system was designed to sit approximately 1 m above the seafloor using subsurface floatation and a removable weight and anchor. A second rope connected the frame to a buoy on the sea surface, with a small line weight attached to the rope just below the surface to reduce the affects of wave action on the movement of the frame.

Stereo-video calibration

Prior to deployment, I tested the stereo-video system in both pool and open water conditions, and calibrated it to define the interior and relative orientations of the camcorders for making measurements (Harvey and Shortis 1998). Calibration was carried out using SeaGIS Pty Ltd CAL software (SeaGIS 2014a, 2014b) in July 2011 in collaboration with the National Institute of Water and Atmosphere (NIWA) Fisheries Acoustics Lab in Wellington. A 3D calibration cube with reflective targets at precisely known positions (Figure 5.3) was recorded underwater in a pool in 20 orientations.

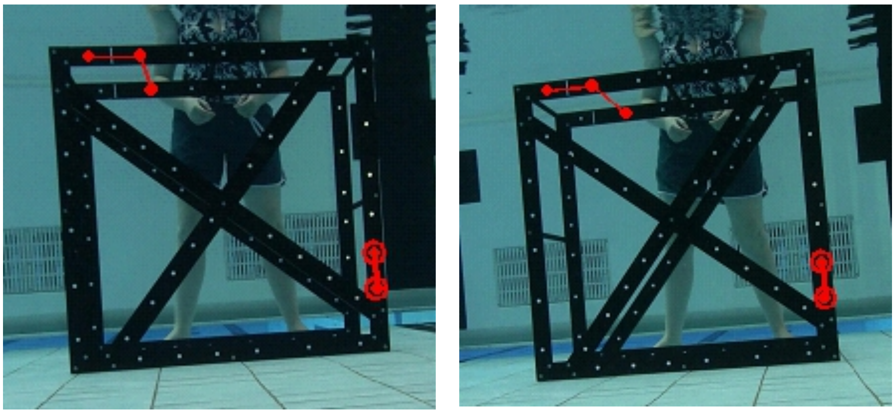

Figure 5.3: A stereo-pair of the SeaGIS 3D calibration cube with reflective targets and measurements in the X, Y, and Z dimensions.

I gathered synchronised pairs of images and measured the location of targets (SeaGIS 2014a). The image data, approximate locations and orientations of the camcorders, and target coordinates were then processed using a photogrammetric bundle solution (Granshaw 1980) to obtain the internal and external camcorder orientations.

In order to test the stability of the measurement system, I conducted three calibrations. In between each calibration I handled the stereo-video frame as it would be during a typical field deployment. Using the bundle solution results from the final calibration, I made measurements on paired images from each calibration using EventMeasure software (SeaGIS 2014b) to examine variation in measurement accuracy and precision between recordings. A series of 30 measurements were made on the calibration cube in each of the X, Y, and Z dimensions (Figure 5.3).

5.2.2 Deployment

I carried out paired deployments around Banks Peninsula between autumn 2011 and summer 2012 during the habitat surveys described in Chapter 4. All were conducted in comparable water depths of 15-20 m. On each sampling trip the trap and stereo-video system were deployed concurrently from a 5.8 m aluminium power boat (R/V Grampus), which moved out of the area after deployment. Both were set approximately 500 m apart to minimise overlap of the bait plumes (Harvey et al. 2007). Data on the time and location of the deployment and retrieval were recorded on a palmtop computer (Hewlett Packard 200LX) with custom software and GPS interface, along with the trap results.

I set both the trap and stereo video system for 3 hours (± 30 min). This allowed sufficient time to retrieve the equipment without typically being disturbed by changes in weather and was deemed to be short enough to avoid escapement from the trap that has been associated with longer soak times (e.g. Whitelaw et al. 1991, Sheaves 1995).

5.2.3 Data collection

Species captured by the traps were identified, counted and measured (by total length or carapace width) upon trap retrieval. I released the majority of the catch alive, but collected and humanely euthanased (Ethics Approval No. ET15/09) some individuals for use in the stable isotope analysis of Chapter 3. If more than ten individuals of any species were present, as was often the case with crustaceans and occasionally fish, the first ten retrieved were measured and the total number caught were recorded.

Ashore, video footage was reviewed by a single viewer using iMovie (Apple Inc., Version 9). The number of each species encountered in a recording was taken as the maximum number individuals observed in a single video frame (MaxN; Willis and Babcock 2000). This avoids recounting individuals that repeatedly pass through the field of view and is considered a conservative estimate of the relative abundance of each species (Willis et al. 2000). Freeze frames were extracted for measurements of individual fish at the time of MaxN for each species, when fish were in the field of view of both camcorders and as parallel to the base bar as possible. Measurements of fish length were made using EventMeasure software (SeaGIS 2014b; Figure 5.4).

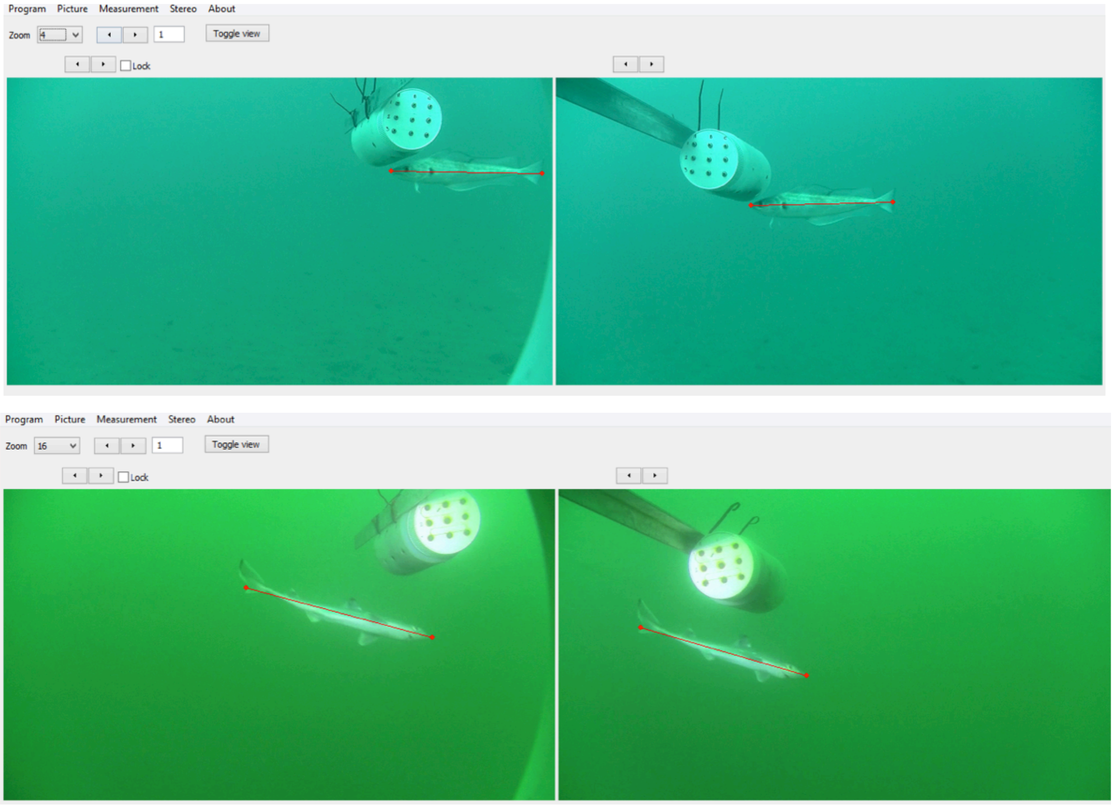

Figure 5.4: Examples of left and right stereo images in the EventMeasure SeaGIS software showing measurements of red cod (Top) and dogfish (Bottom).

5.2.4 Data analysis

I calculated species richness (total number of species) and species diversity (Simpson's Diversity Index: $D=\sum(n/N)^2$) per trap and video deployment. To examine variation in richness, diversity, and species length between methods, I then calculated 95% confidence intervals for the difference between means (Gardner and Altman 1986, Nakagawa and Cuthill 2007). If the confidence interval for a difference contained 0, the data were consistent with no "significant" difference between the two means.

5.3 RESULTS

5.3.1 Stereo-video calibration

Overall, the system achieved very good accuracy when estimating lengths, with measurement error of <1 mm in all dimensions (Figure 5.5). I found no significant variation in the accuracy between recordings (ANOVA: *F*=0.216, *df*=2, *p*=0.806). This implies that typical handling in the field would not affect the quality of measurements.

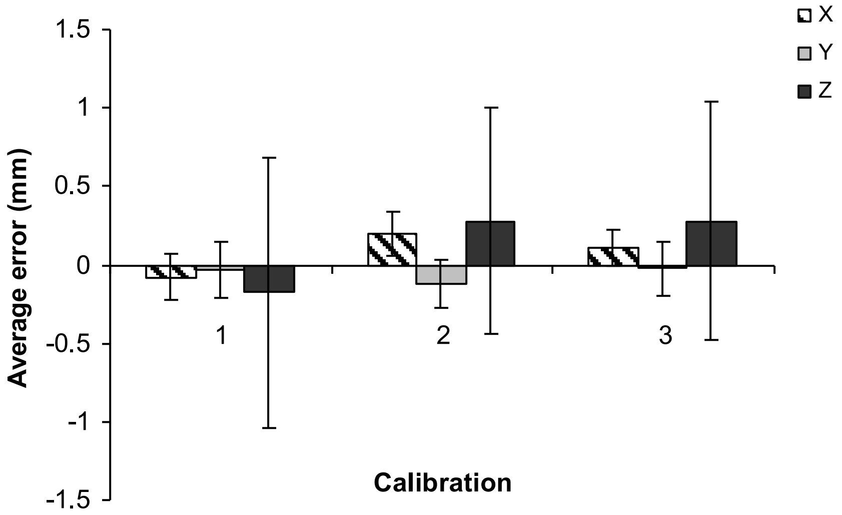

Figure 5.5: The variation in measurement accuracy in the X, Y, and Z dimensions across three calibrations ± SE

There was no evidence for a significant difference in accuracy among the three dimensions measured (*F*=0.129, *df*=2, *p*=0.879). Figure 5.5, however, suggests that measurements in the Z dimension are somewhat less accurate and substantially less precise. Calculation of the coefficient of variation (CV) as a measure of precision (Figure 5.6) confirms this, indicating that the CV for the Z dimensions is greater than the X or Y. I therefore, only made measurements when fish were orientated as parallel to the base bar of the stereo-video frame as possible.

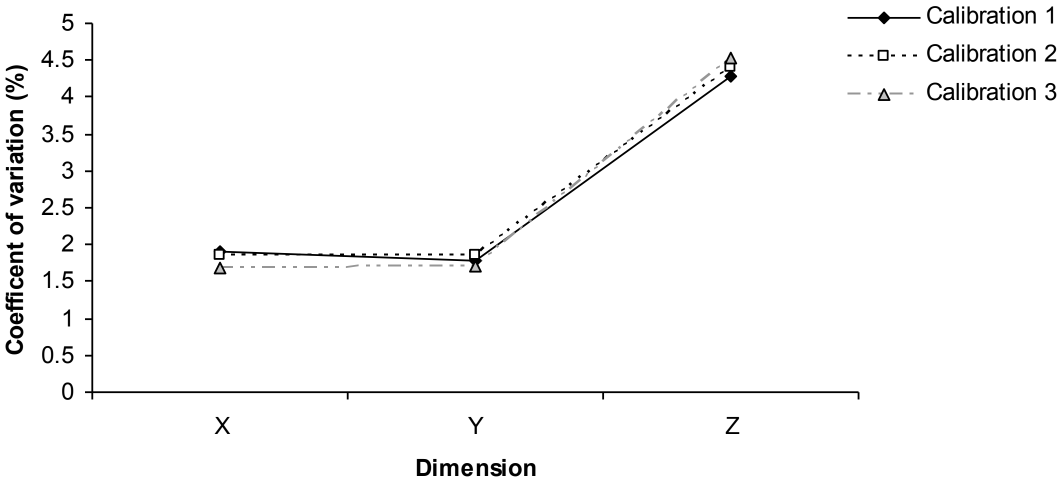

Figure 5.6: Coefficient of Variation (CV) of measurements in the X, Y, and Z dimensions across three calibrations

5.3.2 Comparison between sampling methods

Species richness & diversity

Across all of the 27 paired deployments there were a total of 95 animals from 10 species recorded using stereo-video, and 305 animals from 12 species recorded in the traps (Table 5.1).

Table 5.1: Information on the total and average number of species and individual animals observed in 27 paired stereo-video and trap deployments.

	Total No. Species	**Total No. Individuals**	**Average No. Species ± SE (Range)**	**Average No. Individuals ± SE (Range)**
Stereo-video	10	95	1.4 ± 0.2 (0-3)	3.5 ± 0.7 (0-16)
Traps	12	305	2.5 ± 0.2 (0-5)	11.3 ± 2.8 (0-72)

While traps caught a greater total number of species than were recorded on the stereo-video system, the latter recorded more fish species. Four of these (dogfish, red cod, spotty, and terakihi) were observed using both methods, while a further four fish species (barracouta, blue cod, leatherjacket, and school shark) were only recorded by stereo-video. Dogfish was the species most commonly recorded by stereo-video surveying (Table 5.2). Triplefins were only recorded using the traps (Table 5.2).

A relatively high number of crabs were caught in traps, while none were observed using stereo-video. Of all the fish species, I most commonly caught red cod using traps, and I found this species to be more frequently observed using this method than stereo-video (Table 5.2).

Table 5.2: The abundance (total no. of individuals) and occurrence (no. of deployments) of each species recorded using stereo-video and traps. Average relative abundance ± SE of each species observed per deployment is also shown ('-' indicates no individuals were recorded using that method).

		Total no. individuals (deployments)		**Overall average no. individuals ± SE**	
Species observed		**Video**	**Trap**	**Video**	**Trap**
Squalus acanthias	Dogfish	61 (21)	15 (9)	2.23 ± 0.39	0.56 ± 0.21
Pseudophycis bachus	Red cod	18 (5)	20 (14)	0.67 ± 0.45	0.67 ± 0.15
Galeorhinus galeus	School shark	4 (3)	-	0.46 ± 0.09	-
Nemadactylus macropterus	Tarakihi	4 (1)	7 (2)	0.15 ± 0.15	0.11 ± 0.08
Notolabrus celidotus	Spotty	2 (2)	2 (2)	0.07 ± 0.05	0.07 ± 0.05
Parika scaber	Leatherjacket	2 (2)	-	0.07 ± 0.05	-
Thyrsites atun	Barracouta	1 (1)	-	0.04 ± 0.04	-
Parapercis collias	Blue cod	1 (1)	-	0.04 ± 0.04	-
Eptatretis cirrhatus	Hagfish	1 (1)	-	0.04 ± 0.04	-
Aurelia aurita	Moon jellyfish	1 (1)	-	0.04 ± 0.04	-
Pagurus novizealandiae	Hermit crab	-	136 (8)	-	5.04 ± 2.81
Cominella sp.	Whelk	-	56 (5)	-	2.07 ± 0.97
Metacarcinus novaezelandiae	Piecrust crab	-	54 (17)	-	1.96 ± 0.70
Nectocarcinus antarcticus	Red swimming crab	-	7 (4)	-	0.19 ± 0.12
Forsterygion sp.	Triplefin	-	7 (4)	-	0.26 ± 0.22
Ovalipes catharus	Paddle crab	-	3 (2)	-	0.11 ± 0.08
Notomithrax sp.	Decorator crab	-	1 (1)	-	0.04 ± 0.04
Hippocampus abdominals	Seahorse	-	1 (1)	-	0.04 ± 0.04

On average I caught a greater number of species using traps (Table 5.1) but few species were common. Average species richness was found to be significantly higher in traps than stereo-video recordings (mean difference: 1.11; 95% CI: 0.55 to 1.67; Figure 5.7A), while a slightly higher diversity of species were observed using stereo-video (mean difference: 0.13; 95% CI: 0.04 to 0.22; Figure 5.7B).

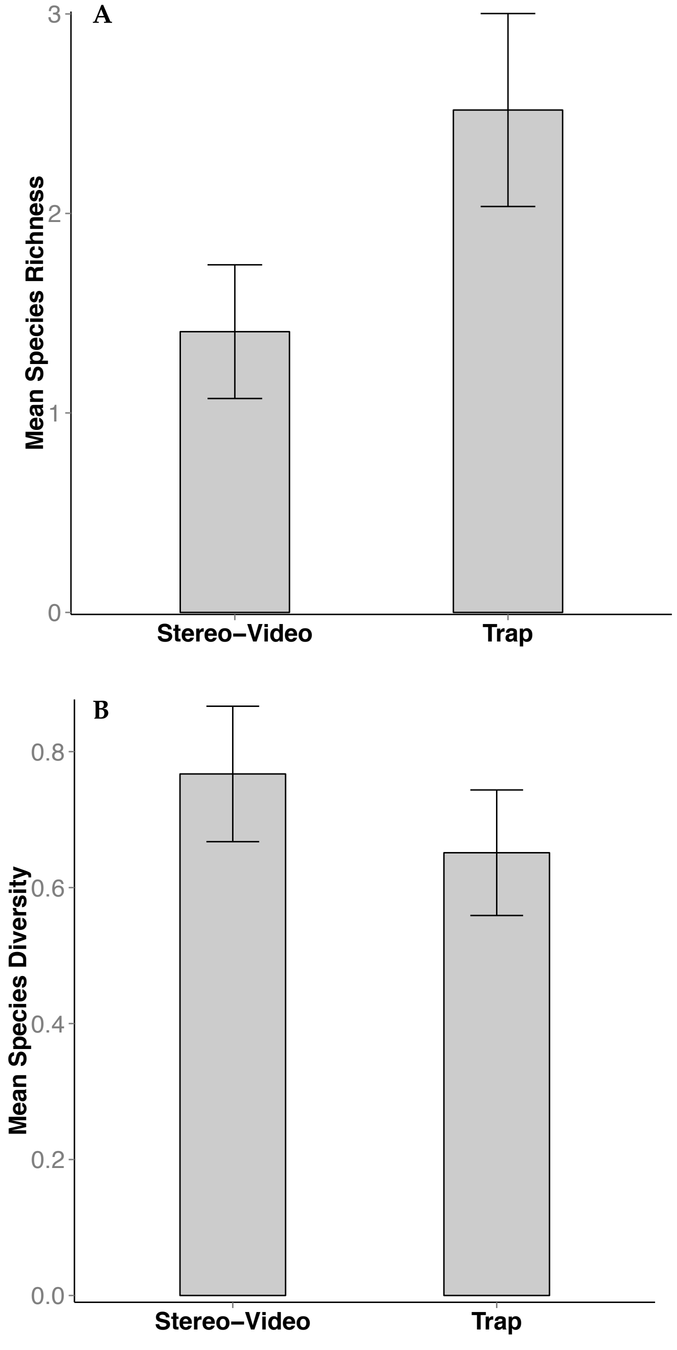

Figure 5.7: Comparison of mean species richness and diversity between stereo-video recordings and traps. Error bars are ± 95% CI.

Size

The mean lengths of dogfish and red cod observed by stereo-video were similar to those captured by traps (Mean difference dogfish: 3.02 cm; 95% CI: -4.52 to 10.55; Mean difference red cod: 11.31 cm; 95% CI: -12.04 to 34.66). Overall, I observed a wider range of fish lengths using stereo-video (4.22 to 68.77 cm) compared to traps (10.5 to 55.3 cm) (Figure 5.8).

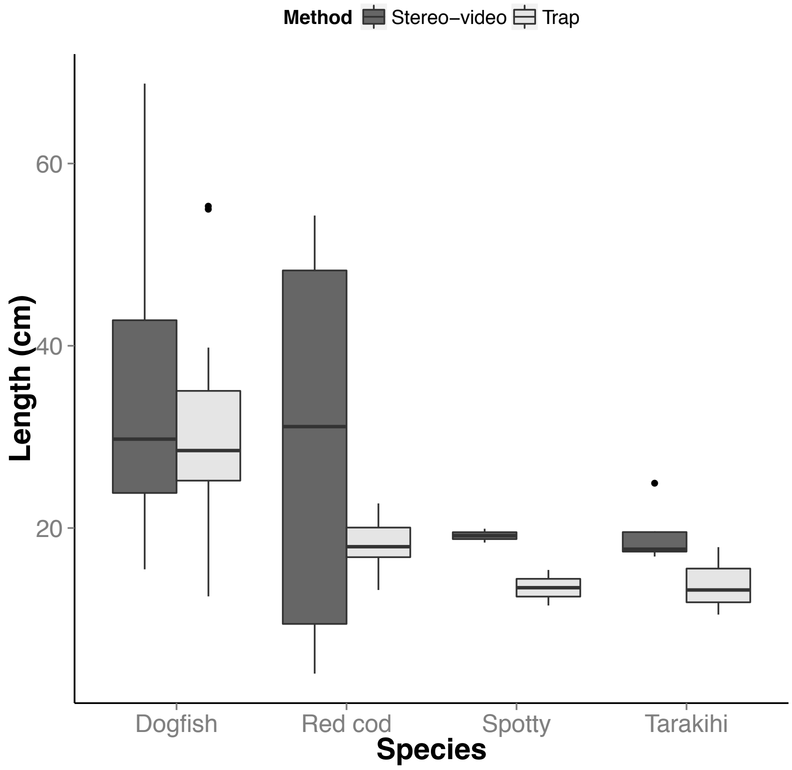

Figure 5.8: Boxplots of the median lengths of the four fish species observed using both stereo-video and traps.

5.4 DISCUSSION

Each method of sampling fish has its own associated biases. Capture techniques can be highly selective and are typically lethal, with traps being the main method that allow fish to be released alive. Remote video systems are gaining wider use as a viable, non-extractive method of sampling fisheries assemblages, but there is a need to understand how their data compares to traditional techniques. Previous comparisons have found stereo-video to be more successful than traps in sampling very small individuals, which can escape through mesh or funnels (Priede et al. 2009). As the majority of Hector's dolphins prey are <20 cm in length (Miller et al.

2013), this suggests that baited video has potential to be a effective method in sampling prey species. Bachelor et al. (2013) also found fish to occur much more frequently on video compared to traps for 11 of the 15 species observed. They suggest this method could therefore be useful in reducing zero-inflation for fish surveys, a common problem in ecological data where an excess of zero responses violate statistical assumptions.

Results reported here show species richness to be higher in traps, largely because they caught more crustaceans, while stereo-video was able to sample a more diverse assemblage of fish species. The traps were in direct contact with the bottom, facilitating access by crabs, while the stereo-video system floated about 1 metre off the bottom. Traps sampled red cod much more frequently, so for surveys such as those of Chapter 4 where this is a target species, traps are likely to be a more effective sampling method. I observed red cod on only a few stereo-video deployments, even though they were often caught in traps nearby. Stereo-video was able to record larger mobile predators such as school shark, and larger dogfish that would have been unable to fit in the traps. An adaptation of this sampling method could be useful in estimating shark presence and predator parameters for future habitat surveys. The use of bait in both methods will most likely attract carnivores, however previous comparative studies have found that baited stereo-video can also provide information on herbivorous species (Watson et al. 2005, Harvey et al. 2007). Within this study, relatively poor visibility is likely to have limited the detection of herbivorous fish as they are less likely to directly approach the bait (Harvey et al. 2007).

In the calibration trials, the stereo-video system achieved very good measurement accuracy, within 0.5 mm on average. There was less precision when measuring lengths in the Z-dimension of the calibration cube. This is usual in stereo-camera systems, and underscores the importance of measuring fish when they are as parallel to the camcorder base bar as possible (Harvey and Shortis 1995). The precision in measurements from stereo-video is better than the approximately 5 mm precision from measuring live trap-caught fish with a ruler on board the vessel, and is considerably less biased than other sampling methods such the use of scale bars in a single-video system (Willis and Babcock 2000) and scuba visual surveys (Harvey et al. 2001, 2002a).

I aimed to target the size range of prey eaten by Hector's dolphin. Overall, the stereo-video system sampled a wider range of fish lengths than the trap, as was found in comparisons by Harvey et al. (2012). The camcorder separation and focal length was designed to give a field of view for measuring small fish. The video system cannot restrict access to fish of certain sizes, as can be achieved in a trap via a combination of funnel size and mesh size. Stereo-video in this study was better able to sample the range of red cod size known to be eaten by Hector's dolphin (2 to 44 cm; Miller et al. 2013), though the red cod in traps were close to the mean length of those consumed (17.9 cm; Miller et al. 2013).

When comparing methods it is important to consider their efficiency and the logistics of each technique. Deployment and retrieval times for both the stereo-video system and trap were approximately 10 minutes. The stereo-video frame took up approximately twice the deck space on the vessel and its larger size required two people to manoeuvre it in and out of the water. Processing time for the video footage was considerable compared to collecting data directly from trap catches. At least one hour was typically spent processing each recording depending upon the number and abundance of fish, aided by fast-forward playback. Trap catch was usually identified and measured on board the vessel within 10 minutes of retrieving the trap. In areas of higher diversity, both methods would likely take considerably longer to process depending on how easy it is to identify species. One benefit of the stereo-video system is the ability to review footage at a later time to confirm species identification, though this could also be achieved by photographing species caught in traps when needed, or retaining specimens. An advantage of the trap is that tissue samples can be taken for additional analyses (e.g. stable isotopes, Chapter 3).

The performance of the stereo-video system was greatly affected by water clarity, while the trap could be used in any level of turbidity. Even moderate turbidity, as was often the case, meant that it was only possible to identify and measure fish within a metre of the camcorders, and so the system relied on fish being attracted to the bait or frame itself. In times or areas of clearer water it is likely that fish passing further away would be observed, as in Harvey et al. (2007) for example, when herbivores were recorded grazing and swimming by 4 to 7 m beyond the bait. It would be interesting to investigate the performance of this system in other areas of the coastline with clearer water, to see if additional species that may not directly approach the camcorders are detected. Overall, the failure rate with the trap was low; only two attempted trap deployments over the course of the study failed when the traps did not set correctly on the seafloor. A total of eleven stereo-video deployments were unusable due to extremely poor visibility.

The distance of attraction of fish to the bait for both the stereo-video system and trap is likely to vary among species, with predatory species expected to move furthest. This makes it hard to define the exact area surveyed by both of these methods, and is important to keep in mind if comparing them to other methods that do not use bait, such as diver surveys or trawls. The lights on the stereo-video system are likely to have attracted some species and not others, and/or altered their behaviour. Harvey et al. (2012) found similar fish assemblages and total numbers of fish were sampled under both white and red light, while Raymond and Widder (2007) found red light decreased disturbance to fish. Future work could assess if the composition of species or number of fish detected changes with red lighting compared to the white lights used in this study.

Neither technique tested in this study was designed to survey cryptic species; both aimed to target demersal prey. To gain a more complete picture of availability of Hector's dolphin prey throughout the water column, it will be necessary to combine such methods with other techniques such as trawling and/or active acoustics. Many trawl surveys around New Zealand are usually carried out well beyond the typical extent of Hector's dolphin distribution. Information available from inshore trawls on the South Island east coast (10-400 m depth) shows dogfish, barracouta, and red cod to have the highest catch rate and occurrence (Beentjes *et al.* 2002). These results are similar to the findings in my study, as dogfish and red cod were the species most frequently recorded by both the stereo-video system and fish traps. Species richness in trawls around the Canterbury region and Banks Peninsula was lower in shallow waters (10-30 m depth) than deeper regions, with around 14 species caught on average (Beentjes *et al*. 2002). There is therefore scope to sample a considerably higher number of species per trawl compared to the methods investigated in this study.

There are many different methods for surveying fish assemblages and prey availability, so it is essential that research objectives are clearly defined for the most appropriate technique to be chosen. Stereo-video is likely to be a more effective technique in areas of consistently better water clarity, and the performance of this system in detecting additional species in such areas should be tested. Overall, the difference in results provided by the fish traps and stereo-video system indicates that a more comprehensive assessment of the mid trophic level community can be obtained by using a combination of sampling techniques.

CHAPTER 6

CONCLUSIONS AND RECOMMENDATIONS

6.1 SUMMARY OF MAIN FINDINGS

The main purpose of this thesis was to study Hector's dolphins in a wider ecosystem context, and identify specific dietary and habitat preferences. My work began by quantifying Hector's dolphin diet using two complementary methods to examine both short and long term patterns. Using this information, I then collected concurrent data on dolphin distribution, prey availability and oceanography at Banks Peninsula to assess which factors influence Hector's dolphin habitat selection.

The stomach content analysis of Chapter 2 (Miller et al. 2013) represented the first quantitative analysis of Hector's dolphin diet and revealed information on the species, sizes, and relative importance of prey. The dolphins were found to feed throughout the water column on a wide variety of species, with 29 taxa identified in total. Their diet appeared to be dominated by a few demersal and mid-water species, with red cod contributing most in terms of mass, and ahuru and lanternfish consumed in large numbers. Small and juvenile prey were targeted, with the majority of prey measuring <10 cm long, and there was evidence of differences in prey between the populations of the South Island east and west coasts.

Stomach content analysis provides information on recently ingested prey. As most samples came from animals that had been killed incidentally in gillnets, most of which were bycaught in summer months, the results were largely representative of the dolphins' diet in summer alone (Miller et al. 2013). To examine the long-term contribution of different prey types to the dolphins' diet, I used stable isotope analysis to quantify dietary patterns on the South Island east coast. As discussed in Chapter 3, stable isotope mixing models of dolphins and prey indicated that bony fish contributed most to the dolphins diet, particularly epipelagic species, such as pilchard. Therefore, while demersal prey such as red cod appear to be most important during warmer months, stable isotope results suggest that epipelagic prey contribute most over the timescale of years. Stable isotope analysis was only able to examine the contribution of prey at a coarse taxonomic level, where prey groupings were isotopically distinct. This, and other limitations discussed in Chapter 3, such as assumptions regarding diet-tissue fractionation, should be considered when drawing conclusions from isotope modelling. Overall, the differences in results between the stable isotope and stomach content analyses highlight the benefits of combining both methods to gain a more comprehensive understanding of dietary preferences.

The influence of prey and oceanography on Hector's dolphin habitat selection was analysed and discussed in Chapter 4. Seasonal changes in dolphin distribution away from shore were similar to those found in previous research (Rayment et al. 2010), with more sightings close to shore and few further from shore in warmer months. Habitat modelling using generalised additive models supported the importance of dietary information, with a combination of data on oceanography and an important prey species, red cod, best describing the patterns in Hector's dolphin distribution throughout three regions of Banks Peninsula. Offshore, alongshore, and within Akaroa harbour, dolphins preferred areas of greater red cod mass. Dolphin distribution offshore was also associated with more saline surface water, and alongshore, dolphins were found in areas of higher prey diversity, higher salinity, and warmer water.

As with dietary analyses, the methods for sampling prey availability each have their own advantages and biases. In Chapter 5, I assessed the feasibility and results of two different methods for sampling the demersal prey of Hector's dolphins at Banks Peninsula. Fish traps, as used in Chapter 4, sampled greater species richness and were more effective at sampling red cod. Baited stereo-video was found to sample greater fish diversity, but was greatly affected by the level of water clarity, which was often poor.

6.2 CONCLUSIONS AND SIGNIFICANCE

Understanding dietary preferences and the drivers behind habitat selection are fundamental in ecology, and greater knowledge of habitat use is particularly important when spatial management measures are used (Hooker and Gerber 2004, Bailey and Thompson 2009), as has been the case at Banks Peninsula since 1988 (Dawson and Slooten 1993), and elsewhere (Slooten and Dawson 2010).

The continued survival of Hector's dolphin relies upon the success of conservation protection measures. Bycatch in bottom-set set nets is the major threat, and has been the main cause of population decline (Dawson 1991a, Slooten 2007, DOC and MFish 2007, Slooten 2013). The Hector's dolphin Threat Management Plan (DOC and MFish 2007) states that two of the main objectives of the protected areas are to "protect key sites in New Zealand waters of significance to Hector's dolphins", and "to achieve self sustaining populations".

Population models show that recovery is unlikely under current protection measures (Slooten and Dawson 2010, Slooten and Davies 2012), largely due to weak protection on the South Island west and north coasts (Slooten 2013). The Banks Peninsula Marine Mammal Sanctuary, while it has resulted in improved survival rates, is also still too small to result in a recovering population (Gormley et al. 2012). Many dolphins are sighted in areas beyond the Sanctuary's 4 n.mi. set net restrictions, particularly in winter (Rayment et al. 2010). Available evidence suggests that to facilitate population recovery and reduce fragmentation, protection measures from set nets and trawling need to be increased throughout Hector's dolphin habitat out to the 100 m depth contour (Slooten 2013), to cover the known depth range of the species (Rayment et al. 2010).

Little is known about the extent and importance of other threats to Hector's dolphins, including indirect fisheries interactions, tourism, mining, aquaculture, and pollution (DOC and MFish 2007, Currey et al. 2012). Hector's dolphins are unlikely to scavenge fish from gillnets, as the sizes of typical Hector's dolphin prey (Miller et al. 2013); Chapter 2) are much smaller than the size of catch selected for by commercial gill net fishers in New Zealand (Hickford et al. 1997). Of the main prey species of Hector's dolphin, red cod is also important to both commercial and recreational fishermen. This species is a target species of the inshore trawl fishery, and biomass trends for the South Island east coast have shown a substantial decline since the mid-1990s (MFish 2007, MPI 2013). While red cod recruitment varies considerably between years, the length and magnitude of decline in catch indicates that fishing pressure may also be responsible for the decreased abundance (MFish 2007). Banks Peninsula has been an important area for the recreational fishing of red cod in the past, but local fishermen have reported that what used to be one of the most abundant species is now a relatively uncommon catch (MFish 2007, MPI 2014). Given that red cod contributed most in terms of mass to the diet of Hector's dolphins (Miller et al. 2013; Chapter 2), and have a strong association with relative abundance of dolphins at Banks Peninsula (Chapter 4), it would be valuable to conduct further research and seasonal monitoring on the red cod population in this area. Use of research trawls, and traps within the habitat range of Hector's dolphins, at a smaller scale than previous surveys (Beentjes et al. 2002), could help assess patterns in seasonal movement and abundance of red cod.

The strong association between seasonal changes in dolphin distribution and the availability of red cod suggests that the dolphins' movements are linked to foraging and driven by the availability of prey. The mass of red cod caught around Banks Peninsula closely matched relative dolphin abundance, with more encountered closer to shore during spring and summer. Inshore areas, including harbours, may therefore be important foraging habitat in warmer months, and so it may be particularly important to manage the level of threats in these areas. Akaroa harbour and the close inshore waters around Banks Peninsula are the main centre for Hector's dolphin tourism (Martinez 2010), which reaches high levels over summer. Martinez (2010) found that dolphins in the harbour during summer only spent a small proportion (14%) of their day in the absence of vessels, and found that diving (inferred foraging) and travelling behaviour were significantly disrupted by interactions with vessels.

6.3 SUGGESTIONS FOR FUTURE RESEARCH

This work has expanded our knowledge of Hector's dolphin ecology. Such work can help build the scientific foundation for conservation tools, but it is important that caution is used before extrapolating results from one population to the species as a whole. To strengthen the predictive capacity of habitat models there are several knowledge gaps that could be addressed, and ideally, further research on Hector's dolphin habitat selection will be conducted for additional populations.

Stomach content analysis (Miller et al. 2013; Chapter 2) indicated differences in prey preferences between the South Island east and west coast populations, and so prey availability may have varying influence on dolphin distribution between these two areas. Small populations such as the dolphins found at Porpoise Bay show strong seasonal movements (Bejder and Dawson 2001). It would therefore be interesting to carry out concurrent prey and dolphin surveys in such areas to see if similar, or perhaps even stronger associations are found. Habitat surveys at Banks Peninsula should be expanded to include additional years of data collection, and additional water depths.

There is considerable scope to extend these habitat models further by surveying the seasonal availability of additional prey species from different habitats. Stable isotope analysis (Chapter 3), suggested that epipelagic bony fish contribute more to the dolphins diet at Banks Peninsula over a timescale of years, and so it would be particularly interesting to include the availability of surface schooling fish in future habitat models. Concurrent surveys of dolphins and epipelagic prey could be achieved by using alternative fishing methods such as active acoustics and small research trawls to identify species. Surveys of schooling fish may also require sampling at finer temporal scales, to examine the predictability and persistence of prey patches (Redfern et al. 2006).

Other potential complementary data to be considered for future habitat modelling is predator abundance. Seasonal movements of Hector’s dolphins could be influenced by predation risk, as was found to be the case for bottlenose dolphins in Shark Bay, Western Australia (Heithaus and Dill 2002, 2006). Further research is needed to determine the nature and risk of shark and killer whale predation on Hector’s dolphins. Continued photo-identification studies and necropsies, examining dolphins for evidence of shark bites, will aid in determining the extent of predation. Further dietary studies of potential predators investigating the extent to which Hector’s dolphin are eaten will also be useful. So far, Hector’s dolphin remains have been found in the stomachs of seven-gill sharks (Cawthorn 1988, Slooten and Dawson 1994), and killer whales in New Zealand waters are known to prey upon other small cetaceans (Constantine et al. 1998, Visser 2007). By monitoring the movements and seasonal abundance of these potential predators in relation to those of Hector's dolphins, it may be possible to identify areas such as shallow bays, which could provide refuge. Other small cetaceans including dusky dolphins have been observed moving close to shore when killer whales are present (Würsig and Würsig 1980).

Investigation of differential habitat use between dolphin sexes and among age classes was beyond the scope of this study, but could be useful in identifying functional drivers of habitat selection. Rayment et al. (2009b) did not find any evidence of clear differences in home range between the two sexes. Webster et al. (2009) however, frequently found Hector's dolphin groups to be segregated by sex and suggest this is potentially due to differences in predation risk or activity budget between males and females.

Due to the opportunistic nature of collecting data on diet, and the associated biases in diet analyses (Miller et al. 2013), the results of both stomach and stable isotope analyses should continue to be expanded upon. Additional samples from other areas and seasons should be analysed whenever possible, and future sampling will help assess any changes in diet over time.

In conclusion, increasing our knowledge of Hector's dolphin ecology and habitat use could help guide management objectives. This study is the first attempt to study Hector's dolphin ecology in relation to their prey, addressing fundamental knowledge gaps in what the dolphins eat, and the role of prey availability in the dolphins' habitat selection. There is considerable scope to extend this work, and doing so could help us further understand and protect the needs of this endangered species. By understanding how the dolphins use their environment; such as which species are important prey, and which areas are important for foraging; managers will be better able to assess how Hector's dolphins will be impacted by a changing environment and design future conservation tools accordingly.

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APPENDIX A

Table A1: Equations to estimate the length (FL: Fork length; TL: Total length) and mass of fish prey from length of saccular otoliths (mm). Equations are in the form $y = Ax^b$.

Family	Genus & species	Common Name			Length equation (cm)			Mass equation (g)		
			n	Fish length (cm)	A	b	r^2	A	b	r^2
Clupeidae	*Sardinops neopilchardus*	Pilchard	Furlani et al. (2007)		3.25	1.370		0.322	4.243	
Clupeidae	*Sprattus antipodum*	Slender sprat	110	FL 3.6-13.4	5.62	0.916	0.97	1.079	3.322	0.97
Engraulidae	*Engraulis australis*	Anchovy	Furlani et al. (2007)		4.71	0.740		0.694	2.501	
Myctophidae	*Lampanyctodes hectoris*	Hector's lanternfish	Jackson et al. (1998)		1.94	1.490		0.064	4.628	
Moridae	*Auchenoceros punctatus*	Ahuru	134	TL 2.8–14.9	1.70	1.498	0.99	0.019	4.674	0.98
Moridae	*Pseudophycis bachus*	Red cod	171	TL 3.2 –73.5	0.83	1.534	0.98	0.004	4.752	0.98
Merlucciidae	*Macruronus novaezelandiae*	Hoki	65	TL 14.5-58.5	1.92	1.178	0.98	0.032	3.384	0.98
Merlucciidae	*Merluccius australis*	Hake	46	TL 5.7-23.1	1.52	1.149	0.97	0.017	3.542	0.97
Macrouridae	*Coelorinchus aspercephalus*	Oblique banded rattail	125	TL 5.9-49.5	1.47	1.250	0.98	0.004	4.241	0.98
Macrouridae	*Lepidorhynchus denticulatus*	Javelinfish	67	TL 11.5-60.5	2.02	1.227	0.98	0.008	4.039	0.98
Trachichthyidae	*Paratrachichthys trailli*	Common roughy	22	FL 14.3-28.5	1.37	1.088	0.94	0.066	3.216	0.91
Cheilodactylidae	*Nemadactylus macropterus*	Tarakihi	59	FL 9.0-46.3	3.37	1.155	0.96	0.466	3.665	0.96
Mugilidae	*Aldrichetta forsteri*	Yelloweyed mullet	82	FL 4.4–37.5	2.91	1.031	0.99	0.163	3.407	0.99
Labridae	*Notolabrus* sp.	Wrasse	20	TL 6.5-38.5	3.16	1.380	0.94	0.125	5.258	0.96
Leptoscopidae	*Leptoscopus macropypus*	Estuary stargazer	19	TL 6.0-30.8	1.50	1.386	0.98	0.022	4.331	0.98
Tripterygiidae	*Forsterygion bathytaton*	Deepwater triplefin	28	TL 4.0-11.3	2.99	0.940	0.97	0.230	3.058	0.97
Eleotridae	*Grahamichthys radiata*	Graham's gudgeon	17	TL 3.7-5.7	5.05	0.600	0.83	0.938	3.196	0.90
Gempylidae	*Thyrsites atun*	Barracouta	90	FL 6.7-52.5	3.46	1.190	0.98	0.150	3.684	0.99
Centrolophidae	*Seriolella brama*	Blue warehou	41	FL 6.7-28.6	2.66	1.072	0.98	0.354	3.162	0.91
Pleuronectidae	*Pelotretis flavilatus*	Lemon sole	36	TL 9.0-38.5	2.83	1.423	0.90	0.588	3.799	0.79
Pleuronectidae	*Peltorhamphus* sp.	Sole	42	TL 5.4-29.8	2.48	1.711	0.93	0.077	5.557	0.95
Pleuronectidae	*Rhombosolea plebeia*	Sand flounder	29	TL 3.0-34.9	2.66	1.675	0.97	2.256	3.510	0.92

Table A2: Equations to estimate the length (FL: Fork length; TL: Total length) and mass of fish prey from length of saccular otoliths (mm). Equations are in the form $y = Ax^b$.

Family	**Genus & species**	**Common Name**	***n***	**Fish length (cm)**		**Length equation (cm)**			**Mass equation (g)**		
						A	**b**	**r^2**	**A**	**b**	**r^2**
Ommastrephidae	*Nototodarus* sp.	Arrow squid	308	DML 3.0-43.5	URL	12.35	0.755	0.99	0.93	2.186	0.93
					LRL	11.89	0.787	0.99	0.79	2.315	0.95
Sepiadariidae	*Sepioloidea pacifica*	Pacific bobtail squid	14	DML 1.9-6.3	UHL	1.12	0.865	0.86	0.17	1.843	0.81
					LHL	1.56	1.021	0.93	0.42	1.970	0.88
Crangonidae	*Pontophilus australis*	Sand shrimp	18	TL 2.0-5.8					0.11	2.950	0.91
Hymenosomatidae	*Halicarcinus* sp.	Pill-box crab	13	CW 4.0-1.1					0.42	2.970	0.94
Macrophthalmidae	*Macrophthalmus hirtipes*	Mud crab	20	CW 1.6-3.2					0.60	2.840	0.98
Portunidae	*Nectocarcinus antarcticus*	Red swimming crab	31	CW 1.1-6.7					0.22	3.050	0.99
	Ovalipes catharus	Paddle crab	14	CW 7.4-12.4					0.18	3.020	0.98